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Bulletin

Torrey Botanical Club

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BACTERIOSTATIC AND BACTERICIDAL PROPERTIES OF ANTIBIOTIC SUBSTANCES, WITH SPECIAL REFERENCE TO PLANT-PATHOGENIC BACTERIA[1]

SELMAN A. WAKSMAN, ELIZABETH BUGIE AND H. CHRISTINE REILLY

INTRODUCTION

The ability of certain microorganisms to inhibit the growth of various bacteria and fungi is due largely to the production of specific agents, designated as antibiotic substances, that possess bacteriostatic or fungistatic properties (9). The bactericidal and fungicidal activities of these substances are not as pronounced, thus distinguishing them from the common chemical antiseptics and germicides.

Both the organisms producing antibiotic substances and the substances themselves are selective in their action upon bacteria and fungi, affecting some species and not others even sometimes in the same genera. These differences in activity are largely quantitative, but they may also be qualitative in nature. Most of the substances so far isolated act primarily upon gram-positive bacteria and only to a limited extent or in much higher concentrations upon gram-negative organisms; other substances, however, act selectively upon some bacteria found within each of these groups. Similar differences are also observed in the action of antibiotic substances upon the fungi. This differential action of a substance upon a number of bacteria is designated as the "antibiotic" or "bacteriostatic spectrum"; each antibiotic substance is characterized by a specific spectrum. When two substances of unknown nature and of different origin have the same spectrum, one is led to assume that they are the same chemically or at least closely related.

The effect of antagonistic microorganisms and antibiotic substances upon plant pathogens has been largely limited to the fungi (3, 4, 5, 9, 19), plant-pathogenic bacteria having been given but scant consideration. The bacterial pathogen was often found to produce a substance bringing about its own inhibition, for example *Pseudomonas destructans*, the cause of turnip rot (6). Other antibiotic agents are produced by soil saprophytes, as certain soil bacteria active against *Ps. citri* (2). Solnzeva (8) demonstrated that myxobacteria are capable of bringing about the lysis of various plant-pathogenic bacteria; a thermostable lytic substance was produced which was not studied further, however.

The ecological relationships of plant pathogenic microorganisms are different in many respects from those of animal pathogens. This is because

[1] Journal Series Paper of the New Jersey Agricultural Experiment Station, Rutgers University, Department of Soil Microbiology.

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the plant pathogens usually are not transmitted directly from one infected individual to another, but largely through an intermediate agency, such as infected seed, wind carried spores, animals, and the soil. The plant pathogen thus often comes in contact with other microorganisms that may exert antagonistic effects upon it, thereby modifying its survival. This is especially true of the soil, where antagonistic microorganisms have an opportunity to grow and produce antibiotic substances, whereby the growth of the pathogen is inhibited or even destroyed. The survival of plant-pathogenic microorganisms in the soil, as influenced by antagonistic microorganisms as well as by antibiotic substances, is of considerable theoretical and practical importance.

No attempt was made to carry out detailed investigations of the effect of a large variety of antibiotic substances upon plant pathogens as a whole or even upon various plant-pathogenic bacteria. A study has been made, however, of the activity of a few substances upon a few bacteria in order to throw some light upon this highly significant natural phenomenon. This is particularly significant since most of the organisms producing these substances are inhabitants of soils or composts. In connection with two comprehensive surveys on the production of antibiotic substances by fungi and actinomycetes (13, 15), several antibiotic agents were isolated. A comparative study was then made (14, 16, 17, 18) of the effect of these agents upon various bacteria comprising both saprophytic forms and human and animal pathogens. The following investigation of the action of some antibiotic substances upon certain bacteria causing plant diseases makes possible broad generalizations concerning the activity of these substances upon bacteria as a whole and upon plant pathogens in particular as compared with saprophytes and animal pathogens.

FORMATION AND NATURE OF ANTIBIOTIC SUBSTANCES

Although the ability to produce antibiotic substances may be characteristic of certain groups of microorganisms and especially of certain genera, only a given species within a genus or even a given strain may be utilized. This is due to the fact that the particular strain may produce the antibiotic substance in sufficient concentration to justify its isolation. Specific strains may be more active under certain conditions of growth and other strains under others (12). Among the fungi, for example, the genera *Penicillium*, *Aspergillus* and *Trichoderma* contain many species that are capable of producing, under certain conditions of nutrition and environment, one or more antibiotic substances. Some microorganisms, like certain yeasts, were found to produce antibiotic agents only in the presence of the antagonized organism. Some of the larger groups of fungi, especially the Phycomycetes and Basiodomycetes, have so far been found to contain only very few forms that have the capacity of producing antibiotic substances.

A fairly large number of antibiotic substances has already been isolated from cultures of different microorganisms. Many of these have been concentrated, but only a few have been crystallized. These substances vary greatly in chemical nature, in mode of action upon bacteria and fungi, in toxicity to animals and in their activity *in vivo*. Some organisms produce more than one antibiotic substance: *Penicillium notatum* forms penicillin and notatin; *Aspergillus flavus*, aspergillic acid and flavicin; *A. fumigatus*, spinulosin, fumigatin and fumigacin; *Actinomyces antibioticus*, actinomycin A and B. Different organisms may also produce the same type of antibiotic substance. Penicillin, for example, was found to be formed not only by strains of *P. notatum* and *P. chrysogenum* but also by *A. flavus* (10). It is still impossible to say definitely how general this phenomenon is, but it is

TABLE 1. *Bacteriostatic spectra of four antibiotic substances.*

Activity, dilution units, thousands per gram

Test organism	Gram stain	Penicillin[a]	Actinomycin[b]	Streptothricin[c]	Clavacin[d]
Staphylococcus aureus	+	9,500*	20,000	200	100
S. aureus	+	1,000†	.....	.....	.....
Sarcina lutea	+	38,000*	60,000	100	500
Bacillus subtilis	+	19,000*	60,000	750	200
B. megatherium	+	1,900*	40,000	200	100
B. mycoides	+	5*	40,000	< 3	200
Clostridium welchii	+	1,500†	1,000	.....	.....
Actinomyces sp.	+	1,000†	10	10–50	.....
Neisseria sp.	–	2,000†	20	.....	.....
Brucella abortus	–	2†	10	100	.....
Shigella gallinarum	–	2†	20	300	.....
Pasteurella sp.	–	1†	< 10	100	.....
Listerella monocytogenes		300	.....	.....	18
Hemophilus sp.	–	.....	50	30	.....
Salmonella schottmülleri	–	< 1†	< 10	200	60
S. aertrycke		10*	.....	.....	.....
Pseudomonas fluorescens	–	< 5*	10	< 3	6
Serratia marcescens	–	< 1	< 5	5	60
Aerobacter aerogenes	–	< 5*	< 5	30	50
Escherichia coli	–	< 1†	.....	.....	.....
E. coli		< 5*	5	100	100

[a] Our own data based on a sample of penicillin having 470 Oxford units are marked *; data reported by Abraham *et al.* (1), based on a less active preparation, are marked †.

[b] Based on data reported elsewhere (17).

[c] Based on data reported elsewhere (18).

[d] Based on data reported elsewhere (14). Much of the above data has been rechecked with fresh preparations.

safe to conclude that antibiotic substances comprise a great variety of chemical compounds, some of which may be formed by more than one organism.

The mode of action of antibiotic substances upon bacteria also varies considerably. Such substances usually interfere with microbial cell division; some affect the metabolic or respiratory processes of the cell; others function as enzymes or interfere with certain enzymatic reactions (10).

The bacteriostatic spectra of four typical antibiotic substances are shown in table 1. Highly concentrated preparations were used, which differed greatly in the degree of purification. Penicillin acts primarily upon gram-positive bacteria and only upon very few gram-negative organisms; however, whereas *Bacillus mycoides*, a gram-positive organism, is only little affected by this substance, *Neisseria* and certain other gram-negative bacteria are sensitive to it. Actinomycin also acts largely upon gram-positive bacteria, with a more gradual transition in the degree of sensitivity between the different groups of bacteria, the cocci and aerobic spore-formers being at one extreme, and *Escherichia*, *Serratia*, and *Pseudomonas* groups at the other. Streptothricin acts upon certain gram-positive and gram-negative bacteria though some organisms within these two groups are only little affected by this substance; there is no important difference in the degree of sensitivity to streptothricin by the gram-positive and the gram-negative bacteria. Clavacin acts nearly alike upon all the bacteria so far tested, with only quantitative differences in the degree of sensitivity of the different organisms; it is also highly active against certain fungi (11). The four antibiotic substances selected at random for this study are thus found to differ greatly in their antibiotic spectra. This justifies the conclusion that the mode of action of each of these substances upon bacteria is different. It may be of interest to recall further that penicillin and streptothricin show only little toxicity to animals, whereas actinomycin and clavacin are highly toxic (7).

NATURE OF ANTIBIOTIC SUBSTANCES USED IN THESE INVESTIGATIONS

Seven antibiotic agents were selected for the following investigations. They were isolated from different organisms naturally occurring in soils or in composts. These organisms were grown upon different media, the nature of the medium and the conditions of growth depending upon the organism, its metabolism, and the environment most favorable to the production of the antibiotic substance. Some substances are produced in synthetic media, others in complex organic media. Some of the organisms were grown in stationary liquid cultures and others in submerged and agitated cultures; some in liquid media and others in semi-solid agar media. Five of the substances were obtained from fungi and two from actinomycetes. The substances used varied greatly in the degree of purification, some being highly

purified and concentrated, and others being crude preparations isolated from the medium and only partly purified.

The nature and potency of these substances can be briefly summarized as follows:

1. *Penicillin.* The preparation used in these experiments was isolated from a culture of *P. notatum.* It was highly concentrated, having 470 Oxford units with *B. subtilis* as the test organism.

2. *Clavacin.* This was a crude and not highly purified preparation isolated from cultures of *A. clavatus* (14).

3. *Fumigacin.* This substance is produced by *A. fumigatus.* Although it has already been crystallized, only a crude preparation was used here. Fumigacin is not readily soluble in water, is active largely against gram-positive bacteria, and is characterized by limited toxicity to animals (14).

4. *Flavicin.* This substance is produced by *A. flavus* and is comparable in its properties to penicillin. A crude preparation containing also a small amount of aspergillic acid was used (12).

5. *Chaetomin.* This material was isolated from an antagonistic strain of species of *Chaetomium* (20). It is characterized by an activity largely directed against gram-positive bacteria, but possesses certain chemical and biological properties that make it quite distinct from penicillin or flavicin, such as high activity against *B. mycoides.*

6. *Actinomycin.* This was a highly purified preparation of Actinomycin A, produced by *Act. antibioticus.* It had an activity of about 10,000,000 *B. subtilis* units (16).

7. *Streptothricin.* Both crude and purified preparations of this material, produced by *Act. lavendulae* (18), were used.

A detailed study of the selective antibiotic action of some of these substances as compared with chemical antiseptics has been published (17).

METHODS

Methods of Testing Bacteriostatic Action. A number of methods are used for measuring the activity of antibiotic substances. They are based largely upon the inhibition of growth and multiplication of specific test bacteria; some of the methods are based upon interference with a physiological reaction of the test organism. The bacteria that are commonly used as test organisms comprise *S. aureus, B. subtilis, Micrococcus* sp., and *E. coli.* The following three methods are employed in making the tests: (a) the streak-plate method, in which several test organisms, differing in the degree of their sensitivity to the antibiotic substances, are used simultaneously; (b) the agar diffusion or cup method, where one test organism is used, usually *B. subtilis* or *S. aureus;* (c) the dilution culture method with only one test organism. The last method was found to be least suitable for this

study. The first has the advantage that the sensitivity of several organisms can be measured on the same plate with different dilutions of the antibiotic substance. The second has the advantage of giving more accurate quantitative results for practical purposes.

The units of measurement reported for the plate method are based upon the dilution of the substance. The minimum concentration of the active material that inhibits growth of the test organism is taken as the end point. The ratio between the volume of medium and the concentration of the active material that is required to bring about inhibition of the growth of the test organism represents the activity units. The zone of inhibition produced on

TABLE 2. *Bacteriostatic action of three antibiotic substances, as measured by two different methods.*

Nature of substances	Purity	Agar-streak method[a]	Agar diffusion (cup method[a])	
			Dilution[b]	Inhibition zone, mm.[c]
		units		
Penicillin	Highly purified material	19,000,000	1: 470,000	22.0
Penicillin	Crude culture filtrate	1,000	1: 25	23.4
Flavicin	Purified	45,000	1: 600	22.0
Flavicin	Crude filtrate	100	Undiluted	23.0
Streptothricin	Purified	750,000	1: 2,000	26.7
Streptothricin	Crude filtrate	300	1: 2	25.5

[a] *B. subtilis* used as test organism in both cases.
[b] On basis of 1 gm. or 1 ml. of material.
[c] Diameter of cup itself – 8 mm.

the plate, expressed in millimeters, is used as a unit of measurement for the cup method. Only for penicillin and streptothricin were standards available; the other substances could be compared against these standards, with one important reservation, namely, that the rates of diffusion of various materials differ; hence no single standard can be employed for comparing the activity of different antibiotic substances.

Ordinary glucose-free nutrient agar media, suitable for the growth of the test organisms were used. The plates were incubated at 30° C for 18–24 hours. The results obtained by the two methods and based upon the use of 3 purified and 3 crude preparations are given in table 2. On the basis of these results, one is justified in concluding that both methods are comparable.

Methods of Testing Bactericidal Action. Several methods are commonly utilized for measuring the bactericidal action of antiseptics and disinfectants. They differ in the nature of the test organism, culture medium or bacterial suspension, and time and temperature of incubation. These methods can be applied with certain modifications to antibiotic substances. However, since these agents are primarily bacteriostatic in nature, whereas their bactericidal action requires a much longer period of time than the ordinary chemical germicidal agents, this phase of the problem was given only limited consideration. A single simple procedure was used as described later.

Strain Variation. Before any generalization can be made concerning the sensitivity of a certain bacterial species to an antibiotic substance, it is essential to establish the variation in sensitivity of different strains within the given species. This becomes particularly significant when one recognizes two well established facts: first, different strains of a bacterial species, difficult to distinguish microscopically, culturally, and physiologically, may show marked variations in the degree of their sensitivity to a given antibiotic substance; second, test organisms may gradually become more resistant to a substance on continuous passage through media containing increasing concentrations of this substance. Certain data pertaining to the sensitivity of different strains of three common spore-forming bacteria to three antibiotic substances are presented in table 3.

The three spore-formers are sensitive alike to clavacin and to fumigacin. The differences in sensitivity obtained for the various strains of each species are greater than between the three different organisms. For example, the average activity of clavacin against *B. subtilis* is 47,000 with variations of 10,000 to 100,000; against *B. mycoides* 39,000 (10,000–75,000); and against *B. cereus*, 17,000 (10,000–25,000). Similar results were obtained for fumigacin. The variation of the sensitivity of the different strains of *S. aureus* against the bacteriostatic action of these two substances was also found to be quantitative rather than qualitative in nature (14). The most striking differences, however, are obtained for streptothricin. *B. subtilis* is highly sensitive and *B. mycoides* is very resistant to this substance, as brought out elsewhere (18). The results presented here show, however, that when several strains of the same organism are used, certain variations are obtained that tend to throw doubt upon the significance of these differences. There were two peculiar exceptions for *B. subtilis*, namely, Nos. 243 and 970.

The sample of streptothricin used in these tests gave for seven strains of *B. subtilis* (except Nos. 243 and 970) a variation of 7,500 to $>$ 33,000 units, with an average of 23,800 units or more; for eight strains of *B. mycoides*, the variation was from $<$ 330 to 5,000, with an average of 2,330 units or

less; for seven strains of *B. cereus*, the variation was from < 300 to 10,000, with an average of 5,000 units or less. It is interesting to note that *B. cereus* overlaps in the degree of its sensitivity to streptothricin the two other spore-forming bacteria, coming much nearer to *B. mycoides*, however. Dr. N. R. Smith, who kindly supplied these cultures, is of the opinion that *B. mycoides* is to be considered as a variety of *B. cereus*. This is well borne out by the results presented here. Of the two exceptional strains of *B. subtilis* that

TABLE 3. *Strain variation among spore-forming bacteria in their sensitivity to antibiotic substances.*

Activity, dilution units, thousands per gram

Organism	Strain No.	Streptothricin	Clavacin	Fumigacin
B. subtilis	0	> 33.0	100	75
"	6	25.0	50	50
"	231	> 33.0	100	50
"	243	< 3.3	50	< 10
"	968	20.0	25	33
"	969	> 33.0	50	75
"	970	< 3.3	20	100
"	971	7.5	20	10
"	972	15.0	10	20
B. mycoides	0	< 0.3	20	10
"	233	2.5	75	100
"	306	2.5	25	50
"	317	2.5	10	50
"	318	0.8	75	15
"	319	2.0	30	20
"	911	5.0	50	15
"	912	3.0	30	10
B. cereus	0	< 0.3	.....	.....
"	201	2.0	10	< 10
"	202	10.0	15	30
"	203	7.5	15	50
"	305	5.0	15	75
"	830	5.0	20	30
"	847	5.0	25	75

showed low activity to streptothricin, one, No. 970, proved to be the so-called Michigan strain, which should really be called *B. cereus*. The other questionable *B. subtilis* strain (No. 243) that gave 2,500 units may either represent an exception from the average or it may be another special case, not as yet recognized.

Although these results are sufficient to emphasize the danger of generalizations concerning the sensitivity of a given organism to an antibiotic substance based upon the testing of a single strain of an organism, it can still indicate broadly the selective action of the substance upon a particular bacterial species.

TABLE 4. *Bacteriostatic activity of different antibiotic substances upon plant pathogenic and other bacteria.*

Activity, dilution units, thousands per gram

Name of organism	Actinomycin	Streptothricin	Clavacin	Fumigacin	Penicillin	Chaetomin
Phytomonas pruni	600	100	300	60	1,000	38
P. tumefaciens	600	150	65	> 90	250	> 1,500
P. campestris	400	15	200	< 3	15	< 15
P. phascoli	1,000	15	200	3	50	15
P. glycinea	> 6,000	50	65	30	150	15
P. syringae	200	> 50	65	3	< 5	45
P. solanacearum	200	5	20	9	> 5,000	> 1,500
P. stewartii	< 60	> 50	200	30	15	< 15
P. michiganensis	> 6,000	15	20	30	500	50
S. aureus	20,000	50	65	> 90	9,500	1,500
B. subtilis	60,000	125	65	200	19,000	350
E. coli	< 60	25	65	< 3	< 5	< 15

	Activity, diffusion method, zone of inhibition											
	Dil.[a]	In-hib.,[b]	Dil.	In-hib.	Dil.	In-hib.	Dil.	In-hib.	Dil.	In-hib.	Dil.	In-hib.
S. aureus	1: 200,000	18.5	1: 600	18.5	1: 3,000	19.0	1: 3,000	20.3	470,000	22.0	1: 500	13.8
E. coli	1: 20,000	0.0	1: 600	16.0	1: 600	14.5	1: 1,500	0.0	470,000	0.0	1: 100	14.5
B. subtilis	1: 200,000	21.0	1: 6,000	19.8	1: 3,000	20.0	1: 3,000	23.0	470,000	20.5	1: 500	16.0
P. phascoli	1: 20,000	17.5	1: 600	26.0	1: 3,000	24.0	1: 1,500	0.0	470,000	0.0	1: 250	14.0

[a] Dil. = Dilution of substance.
[b] Inhib. = Inhibition zone, diameter in millimeters.

BACTERIOSTATIC ACTION OF ANTIBIOTIC SUBSTANCES AGAINST PLANT PATHOGENIC AND SAPROPHYTIC BACTERIA

In this study, 9 plant-pathogenic bacteria, 2 saprophytes, and 2 animal pathogens were compared. These bacteria and their gram reaction are listed as follows:

Organism	*Gram stain*	*Organism*	*Gram stain*
Ph. tumefaciens	–	*Ph. michiganensis*	+
Ph. campestris	–	*Ph. pruni*	–
Ph. phaseoli	–	*E. coli*	–
Ph. glycinea	–	*S. aureus*	+
Ph. syringae	–	*B. subtilis*	+
Ph. solanacearum	–	*S. lutea*	+
Ph. stewartii	–		

Table 4 shows the sensitivity of these bacteria to six of the antibiotic substances, as determined by the agar-streak dilution and the agar-cup diffusion methods. Some of the tests, as for *E. coli* and *B. subtilis*, were repeated many times, whereas others were made only two or three times. It is quite possible that other strains of the same organisms may give somewhat different results.

Actinomycin, with a general high activity against gram-positive bacteria (*B. subtilis* and *S. aureus*) and a limited activity against the gram-negative organisms of the *Aerobacter* and *Escherichia* (*E. coli*) groups, has a marked selective action upon the gram-negative plant pathogens, some of which are very sensitive and others very resistant. The important point to note is that these bacteria do not behave as a group. The gram-negative *P. glycinea* is as sensitive to this substance as the gram-positive *P. michiganensis*, whereas *P. stewartii* is as resistant as *E. coli*. On the other hand, clavacin, which does not show any marked specific differences in activity against gram-positive and gram-negative bacteria in general, shows little difference against the various plant pathogens.

Streptothricin has been found to have a selective action upon bacteria within each group rather than between the two groups as distinguished by their staining reactions. Its action on the plant-pathogenic bacteria proved to be quantitative rather than qualitative, the range of activity varying from 5,000 units for *P. solanacearum* to 150,000 for *P. tumefaciens*. Fumigacin and chaetomin, active largely against gram-positive bacteria and not against *E. coli*, showed considerable activity against some of the plant pathogens and comparatively little activity against others, both within the group of gram-negative bacteria.

Penicillin is known to have little if any activity against most of the gram-negative bacteria. Although some of the plant pathogens showed a certain degree of sensitivity to this substance, this was so limited that even the sen-

sitive cultures (*P. tumefaciens* and *P. phaseoli*) may be considered as fairly resistant when compared with the sensitivity to penicillin of the gram-positive bacteria (*S. aureus, B. subtilis*).

The results obtained by the agar diffusion method show that the plant-pathogenic bacteria fell midway between *E. coli* and the two gram-positive bacteria. There was considerable variation, however, in the degree of resistance of the different bacteria, some being more and others less sensitive. It is to be recalled, in this connection, that gram-negative animal-pathogenic bacteria, such as *Brucella, Pasteurella*, and especially *Neisseria* and *Hemophilus*, are far more sensitive to the known antibiotic substances than are the gram-negative bacteria belonging to the *Escherichia, Aerobacter, Serratia*, and *Pseudomonas* groups.

One may thus conclude that the plant pathogenic bacteria do not behave as a group as regards their sensitivity to antibiotic substances. Despite the fact that most of them are gram-negative, some are more sensitive to certain agents and others more resistant, depending on the nature of the agent as well as of the organism. As a group, however, the plant-pathogenic bacteria of the gram-negative type are similar to the many animal pathogens of the same type, being more resistant than the gram-positive bacteria and less resistant than the gram-negative bacteria of the *Escherichia* type.

Since the substances studied here are not known chemically, their activity cannot be compared on a molar basis. The very fact that they were of different degrees of purity makes it impossible even to compare them on a gram basis. The best that can be done, therefore, is to compare them largely on the basis of their selective activity upon the various bacteria and only very roughly on a weight basis.

BACTERICIDAL EFFECTS OF ANTIBIOTIC SUBSTANCES

The bactericidal action of the antibiotic substances was tested against three different bacteria, namely, *E. coli, S. aureus*, and *P. tumefaciens*. The organisms were grown in nutrient broth for 24 hours at 37° C. One-half-milliliter portions of the cultures were then added to 9.5-milliliter portions of sterile tap water and the antibiotic substances added in dilutions varying from 1:10,000 to 1:100,000. The treated cultures were now incubated at 37° C, and plated after 20 and 40 hours' incubation, nutrient agar being used. The plates were also incubated at 37° C, for 24–48 hours, and the total number of colonies was counted. The counts represent the number of viable and reproducible cells left in each culture. The results are presented in table 5.

Actinomycin, which has only comparatively little bacteriostatic action against *E. coli*, has also limited bactericidal action; even a dilution of 1:10,000 was not sufficient to sterilize the culture completely in 40 hours.

although the number of cells was reduced by about 80 per cent. The same was true of penicillin. Thus both substances, which are characterized by a limited bacteriostatic effect against *E. coli*, have also limited bactericidal action upon this organism. Streptothricin, an agent strongly bacteriostatic against *E. coli*, is also strongly bactericidal; a dilution of 1:100,000 was sufficient nearly to sterilize the culture in 20 hours and completely to sterilize it in 40 hours. The same is true of clavacin, another agent highly active against gram-negative bacteria; however, a larger concentration of this sub-

TABLE 5. *Bactericidal action of antibiotic substances.*
Thousands of bacteria in 1 ml. of diluted culture

Antibiotic substance	Concentration, mgs./10 ml.	Test organism				
		E. coli[a]		*S. aureus*[b]		*P. tumefaciens*[c]
		Incubation hours				
		20	40	20	40	40
Control		140,000	218,000	36,000	252,000	1,020
Actinomycin	1.0	27,700	39,500	< 0.1	< 0.01	< 0.01
Actinomycin	0.1	76,400	111,000	26	2	1.6
Streptothricin	1.0	0.1	< 0.01	1	2	1.8
Streptothricin	0.1	3.0	< 0.01	50	32	3.4
Penicillin	0.5	25,300	26,300	124	69	1.4
Penicillin	0.1	175,000	118,000	360	27	17.0
Clavacin	0.5	650	< 0.01	640	227	1.6
Clavacin	0.1	65,900	54,500	5,000	6,900	343.0
Fumigacin	5.0	7,300	7,500	62	262	1.1
Fumigacin	1.0	80,200	65,000	1,720	270	2.8
Chaetomin	5.0	< 0.1	< 0.01	< 0.01	< 0.01	9.4[d]
Chaetomin	1.0	126,000	188,000	18	185	40.0[d]

[a] Numbers of bacterial cells, in thousands, at start—67,000.
[b] Numbers of bacterial cells, in thousands, at start—10,000.
[c] Numbers of bacterial cells, in thousands, at start— 450.
[d] After 20 hours, control being, in thousands, 198.

stance, namely a dilution of only 1:20,000, was required to bring about complete sterilization of the culture. Fumigacin and chaetomin, substances that are largely active against gram-positive bacteria and exert only a limited bacteriostatic effect on gram-negative organisms of the *E. coli* type, stand midway between the other preparations. In lower concentrations, namely in 1:20,000 dilution, these two substances had little bactericidal action against *E. coli;* in high concentrations, 1:2,000, chaetomin was highly bactericidal and fumigacin also showed some activity.

A totally different relationship was obtained for the bactericidal action of the antibiotic substances against gram-positive bacteria, as represented by *S. aureus*. Actinomycin and penicillin proved to be highly effective bactericidal agents against this organism, the first bringing about a more com-

plete destruction of the bacterial cells. Streptothricin was the only substance that showed somewhat lower bactericidal activity against *S. aureus* as compared with *E. coli;* this is similar to the bacteriostatic properties of this substance. The other three substances exerted about the same type of bactericidal effect upon this gram-positive organism as they did upon the gram-negative *E. coli,* although to a somewhat greater extent.

The bactericidal action of the antibiotic substances against the plant pathogen *P. tumefaciens* was very similar to that against *S. aureus.* The former is somewhat more resistant to chaetomin than the latter. In this respect as well, the bactericidal action of the antibiotic substances is nearly comparable to its bacteriostatic action.

SUMMARY

A comparative study was made of the bacteriostatic and bactericidal effects of several antibiotic substances upon different plant-pathogenic bacteria, two animal pathogens, and two saprophytes, including both gram-positive and gram-negative forms. The antibiotic substances were isolated from antagonistic fungi and actinomycetes and varied greatly in the degree of their isolation and purification.

Plant-pathogenic bacteria were found not to vary greatly in their sensitivity to antibiotic substances from other bacteria. Greater differences were observed among different species than among the various sources from which the bacteria were isolated or their functions under natural conditions.

Some substances, notably actinomycin and penicillin, act largely against gram-positive bacteria and only to a limited extent against gram-negative organisms. In the case of actinomycin the sensitivity of the bacteria ranges from the spore-forming aerobic bacteria and cocci on the sensitive side of the spectrum to the *Escherichia, Aerobacter,* and *Serratia* on the resistant side. Penicillin, however, does not show exactly the same gradation in sensitivity, some gram-negative bacteria like *Neisseria* being sensitive and some gram-positive bacteria like *B. mycoides* being resistant.

Some substances, like streptothricin and clavacin, act alike upon gram-negative and gram-positive bacteria. These two substances also revealed certain marked differences, however, the first being much more selective in its action against the various bacteria than the second. Some gram-positive (*B. mycoides*) and gram-negative bacteria (*Ps. aeruginosa*) are very resistant to streptothricin and others are very sensitive (*B. subtilis, Brucella abortus*).

Two other antibiotic substances, fumigacin and chaetomin, showed intermediate activity upon the different bacteria between that of the other two groups of compounds. Although largely active against gram-positive bacteria and only to a very limited extent against the *E. coli* group, fumigacin and

chaetomin were also active against certain gram-negative organisms, especially some of the plant-pathogenic types.

The degree of sensitivity of bacteria to the various antibiotic substances can, therefore, be only very roughly based upon their staining reactions. The gram-stain is not the absolute determinant of the sensitivity of resistance of bacteria to different antibiotic substances. When more than one substance is tested, it is found that the different bacterial species show distinctly different antibiotic spectra. This points to greater physiological differences among the bacteria, as determined by their relative sensitivity to the antibiotic substances, than can be explained by mere differences in their staining characteristics.

No attempt is made to interpret the significance of the results presented here in terms of possible control of plant diseases caused by bacteria. The fact, however, that the microorganisms from which the antibiotic substances were isolated are normal soil inhabitants, makes these results highly suggestive.

The authors wish to express their sincere appreciation to Dr. N. R. Smith, of the Bureau of Plant Industry, U. S. D. A., for supplying most of the cultures of the spore-forming bacteria, and to W. H. Burkholder, of the Department of Plant Pathology, Cornell University, for the cultures of the plant-pathogenic bacteria.

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RELATIVE GROWTH OF FLOWER PARTS OF TWO SPECIES OF IRIS

HERBERT PARKES RILEY

It has been shown in a number of instances that the pattern of growth of a particular organ may be expressed in terms of the relative growth rates of the main dimensions of that organ. In an extensive comparison of twelve lines belonging to three or four species of cucurbits, Sinnott (1936) showed that the rate of relative growth of ovary length and width was different in each species and that the final shape of the fruit was determined by these rates plus duration of growth. In each case, the relative growth rate remained unchanged throughout the development of the fruit.

In *Iris fulva* and *I. hexagona* var. *giganticaerulea* (Riley 1942) relative growth rates of the main radii of the developing ovary account for the shape of the ovary as seen in cross section and explain why fruits of the two species have different shapes during comparable developmental periods but almost the same shape when they are mature. In each species, the relative growth rate of two radii changes several times throughout development. Relative growth of the radii is due principally to relative growth of the ovary wall at those radii. Riley and Morrow (1942) and Riley (1943) found that in *Iris* ovaries the growth rate of any cellular region such as the ovary wall or the cellular region between two locules is determined by the rate and duration of cell division and the rate of increase in cell size following division but that during most of development cell multiplication is a much more important factor than cell expansion.

The ovaries of these two species are not only very much alike when the mature ovaries are viewed in cross section, but are also not very dissimilar in their general size and shape. The sepals and petals of *fulva*, however, are very different from those parts of *giganticaerulea*. It was the purpose of this study to determine to what extent relative growth rates control the pattern of development of the various flower structures. The plants of *giganticaerulea* are from a marsh alongside Bayou Barataria. Those of *fulva* are from an oak forest-cypress swamp transition at Thibodaux, from a similar region at Laplace, or from an oak forest growing along the side of the road between New Orleans and Bayou Barataria. All are from Louisiana.

Length and width of ovaries, sepals, petals, and floral tubes were measured from fresh material by means of dividers except for the smallest ovaries and tubes. These were fixed, embedded, and sectioned serially, and measurements were obtained from camera lucida drawings of median longitudinal sections. Ovary length was measured from the place where the ovary

is inserted on the flower stalk to the place where it joins the floral tube; measurements of width were obtained from the widest part of the ovary. Sepals and petals were measured from the place where the claw joins the floral tube to the tip of the blade; the width was always the widest part of the blade. It was considered desirable to study the relative growth in length of the claw and of the blade for the sepal and petal of each species. Measurements were plotted of the claws and blades of the sepals, but because the transition from the claw to the blade is more gradual in the petals, the attempt to analyze the relationship of the claw and blade of the petal was abandoned. For each study, measurements were plotted on double logarithmic paper; curves were then plotted by the method of least squares except for very short regions or for those in which the points showed excessive scatter; these were plotted by inspection. The slopes, k, were calculated from Huxley's formula. The original measurements were in tenths of a millimeter and almost all measurements consisted of three significant figures. Four place tables of mantissas were used in converting the original measurements into logarithms. The values of k for the regions that were plotted by least squares were expressed to three significant figures. The slopes for the parts plotted by inspection were expressed in two significant figures.

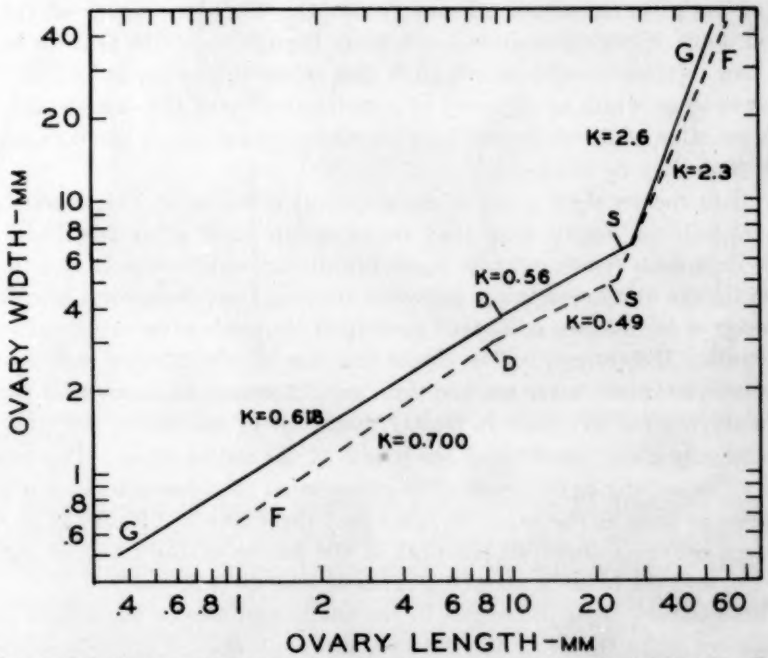


FIG. 1. Relative growth curves of ovary width and ovary length of *Iris fulva* (broken line) and of *Iris hexagona* var. *giganticaerulea* (unbroken line). D, completion of divisions of the nuclei of the embryo sac; S, fertilization.

OBSERVATIONS

Ovaries. When first organized, the ovary of *giganticaerulea* is wider in proportion to its length than is that of *fulva*. During early stages of growth, the ovary of *fulva* grows more rapidly in width relative to length than does that of the other species, but this relationship does not occur over a sufficiently long period for the two species to attain the same proportions (fig. 1). At about the time that the divisions of the nuclei in the embryo sac have been completed, the ovary of *giganticaerulea* is still proportionately wider than that of *fulva* but the difference is not so marked as in earlier stages. At that time the slopes change and the ovary of *giganticaerulea* increases proportionately somewhat more in width than does that of *fulva* until fertilization has been completed. After fertilization the *fulva* ovary is 24 mm. long while that of the other species is 28 mm. in length. When the ovary of *fulva* is 24 mm. long, it begins to grow much more rapidly in width than in length. This new relative growth rate is such that when this ovary is 28 mm. long, it has the same width as an ovary of *giganticaerulea* of the same length. For the remainder of development both ovaries increase much more rapidly in width than they do in length.

In both species the pattern of development is the same. The ovaries grow more rapidly in length than they do in width until after fertilization at which time both fruits increase more rapidly in width than in length. The reason for the first break in the curves is not clear, but the second is probably the result of the sudden and rapid growth of the seeds after fertilization.

Sepals. Differences in the shape and size of the mature sepals of the two species are much more marked than are differences in the ovaries (fig. 2). The mature sepal of *fulva* is mostly made up of the blade, for the claw occupies only about one-fifth of the length of the entire sepal. The blade is about twice as long as it is wide. The entire sepal of *giganticaerulea* is about 1.6 times as long as the sepal of *fulva* and the blade is 1.25 times as wide. The claw occupies about 40 per cent of the length of the sepal of *giganticaerulea*, and the blade is about 1.4 times as long as it is wide.

There is very little difference in the shape and size of the sepals of the two species when they are first formed, although that of *giganticaerulea* is slightly wider. The sepal of *giganticaerulea* increases in length relative to width somewhat more rapidly than does that of *fulva* until late in the development of the bud (figs. 3, 4). At that stage, the sepal of *fulva* is approximately 30 mm. long and the blade is slightly under 15 mm. wide while the sepal of *giganticaerulea* is 49 mm. long and the blade is 20 mm. wide. As the result of the somewhat more rapid growth in length in relation to width in *giganticaerulea* plus the attainment of a greater length, the sepal of *giganticaerulea* is about 2.5 times as long as it is wide, while that of *fulva* is only about 2.1 times as long when the first shift in the curves takes place.

When the sepals have attained this size, there is a very decided change in the slope of each curve and this is shortly followed by a second break in the curve. The slope of the second segment is difficult to interpret accurately as the segment is short and the points that determine the slope are few. This segment has been represented in figures 3 and 4 as a straight, horizontal line, which would indicate that the sepals were growing in length only and that they were not increasing in width during this period of relative growth. While this may not be strictly accurate, certainly the sepals are enlarging

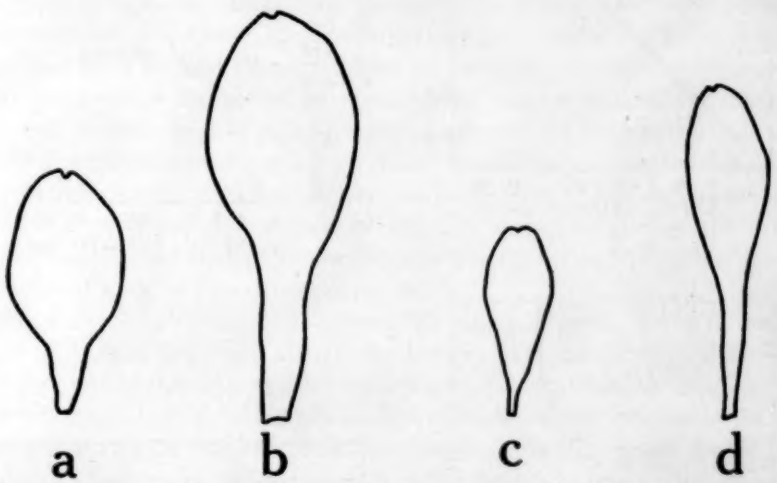
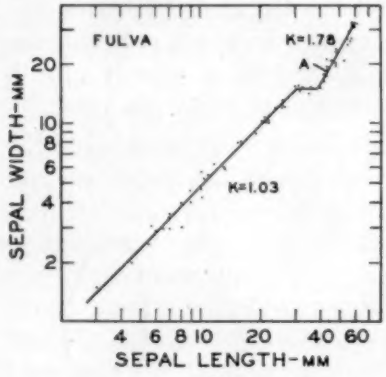
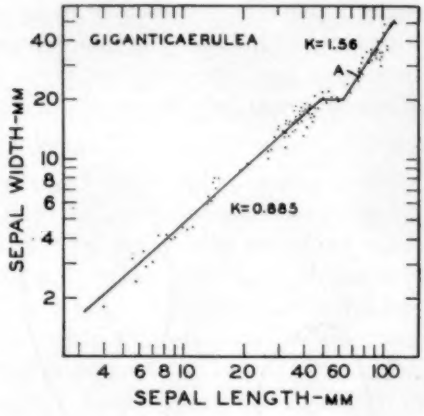


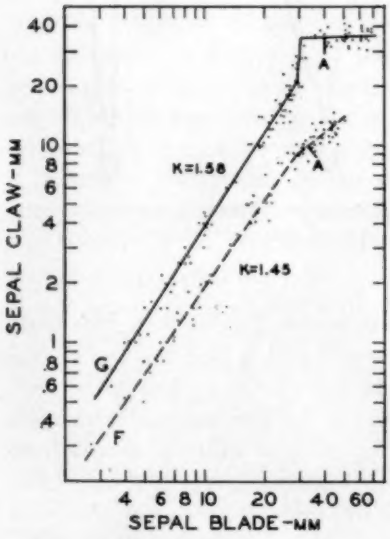
FIG. 2. Outlines of mature sepals and petals; a, sepal of *I. fulva;* b, sepal of *I. hexagona* var. *giganticaerulea;* c, petal of *I. fulva;* d, petal of var. *giganticaerulea.* Approximately × 0.4.

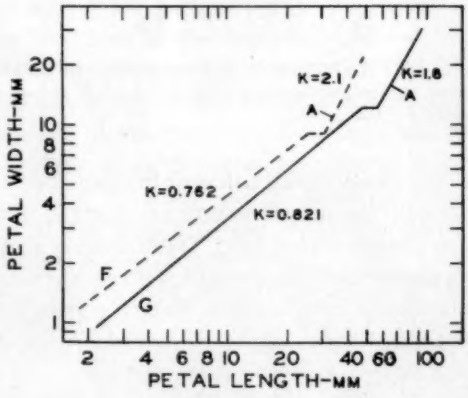
much more rapidly in length than they are in width. To illustrate this more clearly, the actual points are plotted in figures 3 and 4, and the two curves are drawn separately. These double shifts in the curves appear to be real, characteristic features of the two curves and are neither seasonal variations nor clonal peculiarities. Relative growth of length and width of sepals from the same clones of *giganticaerulea* were studied during 1936, 1937, and 1938, and in each year this same feature of the relative growth curve was observed. Plants of *fulva* from Thibodaux were studied during 1937 and 1938; measurements were also obtained and plotted from clones growing in 1936 along the road to Bayou Barataria from New Orleans, and from a group of clones at Laplace in 1937. In all four instances the appearance of the curves was the same. If the interpretation of this double shift in the curves is correct, the sepals of both species increase in length only until that of *fulva* is 39 mm. long and that of *giganticaerulea* is about 65 mm. in length. The blades of the

two species are still about 15 and 20 mm. wide respectively. When the sepals have reached these sizes, growth in width is again resumed. Until the flowers wither, the sepals of both species grow considerably more rapidly in width than in length.









FIGS. 3–6. Relative growth curves. FIG. 3. Sepal width and sepal length of *I. fulva*. FIG. 4. Sepal width and sepal length of *I. hexagona* var. *giganticaerulea*. FIG. 5. Length of claw of sepal and length of blade of sepal of both species. FIG. 6. Width of petal and length of petal of both species. A, anthesis.

The differences in the shape of the sepals of the two species at corresponding states of the development of the flower are due in part to differences in

the slopes of the lines in comparable parts of the curves but even more to the fact that the sepals of *giganticaerulea* become much larger than do those of *fulva*. For example, when the sepal of *fulva* is 30 mm. long, it is 2.04 times as long as it is wide, while a sepal of *giganticaerulea* of the same length is 2.33 times as long as it is wide. The difference in small part is due to an initial size difference but is due mostly to differences in relative growth rates. However, sepals of flowers in the same stages of development rather than sepals of the same length should be compared. A comparison of sepals 30 mm. long in the two species does not have much meaning for such a sepal is found in a flower of *fulva* in which the divisions of the embryo-sac nuclei have been completed but in a flower of *giganticaerulea* in which the four microspores have just been formed. When flowers of the two species are compared in which the embryo sac nuclei have completed their divisions, the picture is different. Such flowers of *giganticaerulea* are 49 mm. long and are approximately 2.5 times as long as they are wide. Therefore, not only differences in the relative growth rates but differences in the size of the structures at the same stage of development must be considered, provided that the relative growth rates do not change before this size is attained and provided also that the value of k in the two curves is not unity.

Since the sepal consists of two rather distinct parts, the claw and the blade, and since these two structures are proportionately very different in the two species, an analysis of the claw-blade relationship is of interest. Figure 5 shows that in *fulva* the claw grows more rapidly than does the blade until shortly before anthesis at the time when the second break occurs in the curves of sepal width against sepal length. The blade is initially almost ten times as long as the claw. Since this relative growth rate does not operate for a sufficiently long period, the claw never equals the blade in length, but at the time of the change in the slope of the curve, the blade is only about 3.2 times as long as the claw. During the remainder of development, the blade increases more rapidly than does the claw.

In *giganticaerulea*, the picture is very different (fig. 5). The sepal blade is initially about five times as long as the claw. The claw grows at a more rapid rate than does the blade, until the entire sepal is about 50 mm. long, at which time the blade is only about 1.25 times as long as the claw. There is then a very rapid increase in the length of the claw relative to that of the blade. The exact slope of this segment of the curve cannot be determined, but there is no doubt that the claw is growing relatively much more rapidly. When the sepal is about 65 mm. long, the blade is only about 0.86 times as long as the claw. The slope of the curve then shifts again, and the blade grows very much more rapidly than the claw. It is very difficult to determine the exact slope of the last two segments of this curve because the segments are short and the points are either too few or show too much scatter.

It is possible, however, that during the second segment of the curve there is practically no growth of the blade, while during the third segment, there is almost no growth of the claw.

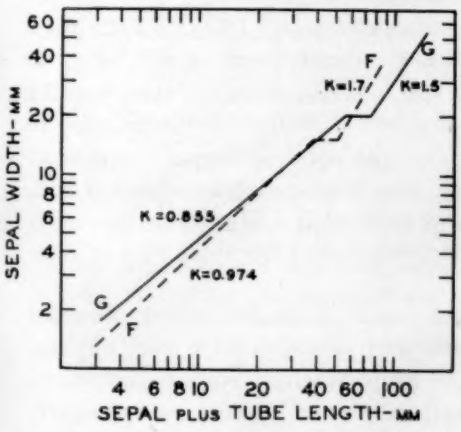
Undoubtedly, the difference in the claw is an important factor in determining the difference in the general shape of the sepals of the two species. When figures 3, 4, and 5 are studied together, the picture of sepal development is essentially the same in both species, except for relatively small differences in initial shape and in relative growth rates, until late in the development of the bud. From then until shortly before anthesis, the blade of *fulva* ceases to increase in width but both blade and claw continue to elongate and at the same relative rate as previously. In *giganticaerulea*, however, the blade ceases to grow both in width and in length, while the claw elongates considerably. The sepal of this species has a more spindly appearance in a late bud. During the opening of the flower, the sepal increases in width in both species; in *fulva*, both the blade and claw elongate, while in *giganticaerulea* the claw has ceased to grow in length.

Petals. Like the sepals, the mature petals differ considerably in shape in the two species, for that of *giganticaerulea* is about 1.75 times as long as that of *fulva* and very little wider (fig. 2). The claw of the petal of *giganticaerulea* is actually and proportionately much longer than the claw of the petal of *fulva*. When they are first organized, the petals of *fulva* are considerably wider than are those of the other species although the lengths are approximately the same. The petals of both species grow more rapidly in length than they do in width until late in the development of the bud (fig. 6). At this time the *fulva* petal is 25 mm. long and is 2.8 times as long as it is wide, while that of *giganticaerulea* is 47 mm. long and is 3.9 times as long as it is wide. At this stage of development of the flower, the petal of *giganticaerulea* is not only very much longer than that of *fulva* but is also considerably longer in proportion to its width.

When the petals have reached this size, there is a double shift in the curves similar to the situation found in the curves of length and width of the sepals, and apparently the petals grow in length but not in width for a short period of the life cycle. During the last stages of the growth of the bud and during the expansion of the flower, the petals of both species grow much more rapidly in width than they do in length. The appearance of the curves of the same clones of *giganticaerulea* during three successive years is similar. The curves of *fulva* from Thibodaux during two different years and those from plants near Bayou Barataria in 1936 and from Laplace in 1937 were also similar. The general pattern of development of the petals is similar to that of the sepals, but there are considerable differences in the slopes and in the y-intercepts of the first and third segments of each species.

Sepal and Petal. When first measurable, the sepal of *fulva* is about 1.35 times as long as the petal of the same species. These two structures grow at almost the same rate ($k = 1.02$; $b = 0.72$) throughout development, so that when mature, the sepal is about 1.30 times as long as the petal. The relative sizes and relative growth rates are slightly different in the other species. When first organized, the sepal of *giganticaerulea* is 1.5 times as long as the petal. The petal elongates somewhat more rapidly than the sepal ($k = 1.07$; $b = 0.62$), and in the mature flower, the sepal is only about 1.2 times as long as the petal. In each species the relative growth rate is unchanged throughout development. The values of k are only slightly different in the two species and this slight difference might be due only to chance and therefore have no significance. However, for these two curves the points show remarkably little scatter and it is possible that the difference is real although not pronounced.

Floral Tube. In both species the floral tube increases much more rapidly in length than it does in width, measured at its greatest width. In *fulva* when



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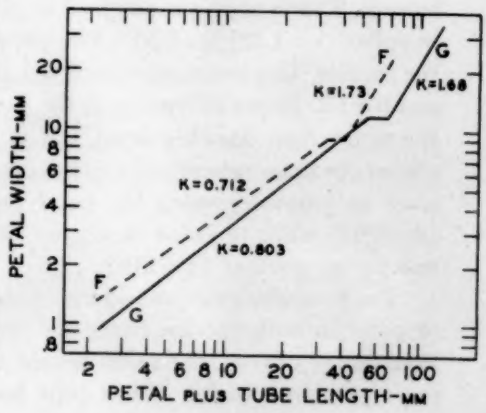

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FIGS. 7, 8. Relative growth curves. FIG. 7. Width of sepal and combined lengths of sepal and floral tube. FIG. 8. Width of petal and combined lengths of petal and floral tube. Broken lines are curves of *I. fulva* and solid lines are curves of *I. hexagona* var. *giganticaerulea*.

tube width is plotted against tube length the slope of the line is 0.22 ($b = 1.62$) and in *giganticaerulea* it is 0.19 ($b = 2.11$). In each species there is no change in the relative growth rate during development. Since the floral tube is often considered to consist of part of the perianth and part of the stamens, the length of the floral tube was plotted against the length of the sepal above the floral tube and the greatest width of the sepal blade was plotted against the length of the sepal plus the length of the floral tube.

Tube length was also plotted against petal length, and the width of the blade of the petal was plotted against the combined lengths of petal and floral tube.

The tube elongates considerably more rapidly than does the sepal in each species. In *fulva*, $k = 1.62$ and $b = 0.028$, while in *giganticaerulea*, $k = 1.42$ and $b = 0.032$. The curves of sepal width against sepal length plus tube length (fig. 7) are generally similar to those of sepal width against sepal length alone, although the slopes and y-intercepts are somewhat different. It is to be expected that the curves might be similar, for the tube is relatively short when compared with the sepal. The relative growth curves of tube length against petal length are a single straight line for both species, but the slopes are considerably different. For *fulva*, $k = 1.60$ and $b = 0.048$, while for the other species, $k = 1.35$ and $b = 0.061$. The curves of petal width against petal length and tube length combined are in general similar to those of petal width against petal length although, as in the case of the sepals, the values of k and b are different (fig. 8).

Other Relationships. The sepals elongate more rapidly than do the ovaries. This is more pronounced in *giganticaerulea* ($k = 1.42$; $b = 1.02$) than in *fulva* ($k = 1.32$; $b = 1.55$). The petals also elongate more rapidly than do the ovaries. In *giganticaerulea*, $k = 1.49$ and $b = 0.70$, while in *fulva*, $k = 1.25$ and $b = 1.1$. In *giganticaerulea*, the petal grows slightly faster in relation to the ovary than does the sepal, but in *fulva* the petal and sepal elongate at almost the same rate relative to the ovary. This relationship is to be expected, since in *giganticaerulea* the petal grows somewhat faster than the sepal ($k = 1.07$) while in *fulva* they grow at approximately the same rate in relation to one another ($k = 1.02$).

The tube elongates considerably more rapidly than does either the sepal or petal in both species. Since the sepals and petals enlarge more rapidly than do the ovaries, the tubes should also grow in length more rapidly than the respective ovaries. When tube length is plotted against ovary length, $k = 1.93$ and $b = 0.035$ in *giganticaerulea*, while $k = 2.22$ and $b = 0.052$ in *fulva*.

Relative Growth Rate Ratios. An interesting relationship which may or may not have significance is found when the slopes of the various curves or segments of curves of *fulva* are divided by the slopes of the corresponding curves or segments of *giganticaerulea*. The quotients that are obtained for most of the curves and segments are listed in table 1. This table includes all the curves or segments of curves except those which would result in a ratio in the indeterminate form 0/0, or the second and third segment of the curve of sepal claw against sepal blade where the slope of *giganticaerulea* is close to infinity or approximately zero. Nineteen quotients are listed for nineteen segments or curves which have been studied. They can be divided into four

groups. Ten curves or segments have a ratio between 1.13 and 1.19. It is possible, of course, that these actually represent six different ratios, but these ratios taken together show a deviation of only six in the third significant figure. This deviation does not seem too great to be due to chance and it seems reasonable to consider that these are all examples of one relative growth rate ratio between two species. One segment of one curve has a ratio of 1.03. This rate is found for the third segment of the curve of petal width against petal length plus tube length. The third segments of some of the curves are short and their points show some scatter, so it is possible that this segment and

TABLE 1. *Relative growth rates and relative growth rate ratios for nineteen curves or segments of curves.*

Ratio	Curve	Relative growth rates	
		fulva	*giganticaerulea*
1.19	Tube length and petal length	1.60	1.35
1.17	Petal width and petal length, segment III	2.1	1.8
1.16	Tube width and tube length	0.22	0.19
1.15	Tube length and ovary length	2.22	1.93
1.15	Sepal width and sepal length; segment I	1.03	0.885
1.14	Sepal width and sepal length, segment III	1.78	1.56
1.14	Sepal width and sepal plus tube, segment I	0.974	0.855
1.14	Tube length and sepal length	1.62	1.42
1.13	Sepal width and sepal plus tube, segment III	1.7	1.5
1.13	Ovary width and ovary length, segment I	0.700	0.618
1.03	Petal width and petal plus tube, segment III	1.73	1.68
0.95	Petal length and sepal length	1.02	1.07
0.93	Petal width and petal length, segment I	0.762	0.821
0.92	Sepal claw and sepal blade, segment I	1.45	1.58
0.89	Petal width and petal plus tube, segment I	0.712	0.803
0.89	Ovary width and ovary length, segment III	2.3	2.6
0.88	Ovary width and ovary length, segment II	0.49	0.56
0.87	Sepal length and ovary length	1.23	1.42
0.84	Petal length and ovary length	1.25	1.49

therefore its ratio are not so accurate as some of the other ratios. Three curves or segments have a ratio between 0.92 and 0.95 and may possibly be considered together. Five ratios vary from 0.84 to 0.89, and possibly represent one fundamental ratio.

If there were no relationship in relative growth between the two species the nineteen curves or segments could give nineteen different ratios and it is probable that at least a large per cent of the ratios would be different from one another. If the interpretation is admissible that the nineteen ratios can be grouped into four basic ones in which the variation is no greater than would be expected from random sampling and errors in measurements, a fundamental species relationship is indicated. It might be pointed out that in some cases it would be expected that the ratios would be the same because

of the nature of the curves. For example, the curves of sepal width against sepal plus tube should not be very different from the curves of sepal width against sepal length because tube length is proportionately very small when compared with sepal length. Such cases, however, are few. The fact that such different relative growth rates as tube width and length, sepal width and length, one segment of the curve of petal width and length, ovary width and length, tube length and petal length, and tube length and ovary length produce the same ratios would seem to indicate, at least, that there is a relationship between these species that expresses itself in the relative growth rates of various structures. The relative growth rate *ratios* of many curves or segments are the same even though the relative growth *rates* vary from 0.22 for tube width and length of *fulva* to 2.22 for tube length and ovary length of *fulva*. The fact that so many of the ratios are the same even though the rates themselves are very different supports the idea that a fairly simple relationship exists in the development of form in these two species.

SUMMARY

The ovaries of *Iris fulva* and *Iris hexagona* var. *giganticaerulea* grow more rapidly in length than in width until after the completion of the divisions of the nuclei in the embryo sac. From that time until after fertilization, growth in length is relatively even more rapid than previously. During fruit enlargement, the ovaries grow much more rapidly in width than in length. The rates are different in the two species for corresponding periods of development.

In *I. fulva,* sepal length, measured from sepal tip to the junction of the claw and floral tube, and sepal width grow at almost the same rate until fairly late in the bud; during this period the claw grows more rapidly in length than does the blade. During a short period before the opening of the flower, growth in width ceases and the sepal grows in length only; the relative growth rate of the claw and blade is the same as previously. During the opening of the flower, the sepal enlarges much more in width than in length and the blade grows more rapidly than the claw.

In var. *giganticaerulea,* the sepal grows more rapidly in length than in width and the claw grows much more rapidly than does the blade until a fairly late bud stage. The blade then ceases to grow in either dimension while the claw continues to elongate, so that, during this period, the sepal as a whole grows in length only. During the opening of the flower the claw does not grow, but the blade resumes growth and the sepal as a whole grows more rapidly in width than in length.

In each species the petals grow more rapidly in length than in width until the bud is almost fully grown. The petals then apparently increase in

length only until shortly before anthesis. During the last phase of development, the petals increase considerably more rapidly in width than in length.

In *I. fulva*, the petals and sepals elongate at almost the same rate but in var. *giganticaerulea* the petals increase in length a little more rapidly than do the sepals. The difference in the slope in the two species is very small.

The floral tube increases much more rapidly in length than in width in each species. The tube elongates more rapidly than does the sepal. The curve of sepal width against sepal length plus tube length is, in general, very similar to the curve of sepal width against sepal length alone in both species. Similarly, the curves of petal width against petal plus tube resemble those of petal width against petal length, although in the case of both sepal and petal the slopes and y-intercepts of the first and third segments are different.

In both species, the sepals, petals, and floral tubes elongate more rapidly than do the ovaries.

For nineteen curves or segments of curves, the slope of *I. fulva* was divided by the slope of var. *giganticaerulea* to produce a relative growth rate ratio. Allowing for errors of sampling and measurement, these nineteen curves or segments can be grouped into four basic ratios. Ten curves or segments have a ratio from 1.13 to 1.17; one has a ratio of 1.03; three have a ratio from 0.92 to 0.95; and five have a ratio of 0.83 to 0.89. Similar ratios are found even for different structure such as ovaries, sepals, and petals, and even though the relative growth rates, themselves, in many instances, are widely different. This constant repetition of a few ratios probably indicates a simple growth rate relationship between the two species.

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INFLUENCE OF LIGHT ON THE INFECTION OF WHEAT BY THE POWDERY MILDEW, ERYSIPHE GRAMINIS TRITICI

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The work of Reed (1914), who concluded that the effect of light on the infectiousness of barley and wheat mildews was due to the influence of the light on the development of chlorophyll in the host plant, suggested a close connection between mildew infection and the carbohydrate supply in the host.

Trelease and Trelease (1929) verified this connection. They found that the powdery mildew, *Erysiphe graminis tritici*, easily infected wheat leaves in either light or darkness provided an adequate source of carbon was available, and they concluded that there is a direct correlation between mildew development and the amount of carbon available in the host. More recently Allen (1942) has furnished interesting quantitative evidence that in heavily infected leaves carbohydrate is the primary substrate that is oxidized, although toward the end of the infection other substrates are also oxidized. Trelease and Trelease (1929) also showed that inoculated plants in the light but deprived of carbon dioxide were incapable of supporting mildew, but that if these same plants were supplied with appropriate sugar solutions, the mildew developed despite the lack of carbon dioxide. The fungus evidenced no tendency to spread into the solution but remained strictly limited to the host. Yarwood (1934a) noted a similar phenomenon and observed that within limits the susceptibility of clover leaflets to species of *Erysiphe* increased as the concentration of the sugar solution on which the leaflets were floated increased. The primary purpose of the present investigation was to study quantitatively the effect of different daily periods of illumination on the infection of wheat, *Triticum vulgare*, by the powdery mildew, *Erysiphe graminis tritici*.

The comparative freedom of plants from mildew infestation in sunny seasons or locations has been attributed not only to the relatively high temperatures then or there prevailing but, in part at least, to ultra-violet radiation in sunlight. Hey and Carter (1931), using a quartz mercury vapor lamp as a source of ultra-violet radiation, were sometimes able to check partially an attack of mildew without appreciably injuring the host plant. In the present study, the influence of different spectral regions upon spore germination was also investigated.

METHODS

The methods employed were the same as those previously described (Pratt 1943). Hanging-drop cultures were used for studies involving the fungus alone, and for studies involving mildew cultures on the host plants a thermostatic chamber (Trelease 1925) so arranged that it could be illuminated from above was employed. The techniques of inoculation and of culturing stock plants were the same as those used previously (Pratt 1943).

RESULTS

Development of Mildew on Living Plants under Different Daily Periods of Illumination. To ascertain the minimum daily exposure to light that would permit mildew development on wheat plants under the experimental conditions, plants that had been in darkness for 24 hours to free them of surplus carbohydrates immediately before treatment were inoculated in the usual manner and then were subjected to different periods of illumination. The source of light was a 1000-watt clear Mazda-C electric light lamp provided with a reflector that was suspended approximately four feet above the plants. The data that were obtained are shown in table 1.

TABLE 1. *Effect of day length upon incubation period and maturation period of powdery mildew on Marquis wheat.*

(1) Temp.	(2) Daily illumination, hours	(3) Av. incubation period,[a] days	(4) Av. time for appearance of conidia, days	(5) Av. maturation period,[b] days	(6) Maturation Period / Incubation Period	(7) Virulence of infection (approximate)
10° C	1	7.75	12.50	4.75	0.613	+
	3	7.25	11.50	4.25	0.587	+++++
	6	6.75	10.25	3.50	0.519	+++++
	12	6.50	10.00	3.50	0.538	+++++
	24	6.25	9.25	3.00	0.480	+++++
20° C	1	3.25	5.00	1.75	0.539	+
	3	2.75	4.00	1.25	0.455	+++
	6	2.50	3.50	1.00	0.400	+++++
	12	2.25	3.00	0.75	0.333	+++++
	24	2.50	3.50	1.00	0.400	+++++
25° C	1	3.75	6.00	2.25	0.600	+
	3	3.25	4.50	1.25	0.384	+++
	6	2.50	3.50	1.00	0.400	++++
	12	2.50	3.75	1.25	0.500	+++++
	24	2.50	3.75	1.25	0.500	+++++

[a] Time elapsed between inoculation of the plants and the first macroscopic signs of infection.

[b] Time required for appearance of first conidia minus incubation period.

No readily distinguishable differences in the virulence of the infection that finally occurred were observed until the period of illumination was reduced to three hours daily at 20° and 25° C, or to one hour daily at 10° C, although a notable delay in the time required for development was noted at 10° C when the plants were illuminated less than six hours in each twenty-four. It is probable that under the experimental conditions used about one hour is the minimum daily exposure to light which will permit elaboration by the host of sufficient requisite materials to maintain it in a condition suitable for support of mildew. Abundant development of the mildew did not occur at any temperature when plants were illuminated less than three hours daily. The decreasing trends, of the values given in column 6, indicate a tendency for the length of the maturation period with respect to the incubation period (both periods being determined purely arbitrarily) to decrease with increasing daily periods of illumination, at least for cultures at 10° C and 20° C. The data for cultures at 25° C are somewhat erratic, but they may indicate a similar trend.

The virulence of infection with a three hour daily period of illumination was greater at 10° C than at 20° C or 25° C (column 7). Possibly this is correlated with the relative rates of respiration and of photosynthesis in the host. Development of the parasite undoubtedly depends upon the ability of the host tissues to furnish a continuous supply of suitable nutrient substrates. In view of the obligate parasitic habit and the high degree of physiological specialization of the fungus, it is reasonable to assume that some of its essential metabolites are compounds that are in no way by-products, but are essential reactants in some step of the metabolism of the host. One can, therefore, think of the host and the parasite as competing for some essential substrate. At the higher temperature, destruction of this substrate or some important intermediate in the host might very conceivably proceed more rapidly than its synthesis. Thus a deficiency of the requisite compounds might occur. Possible support for this suggestion is offered by the generally somewhat higher Q_{10} values for respiration than for photosynthesis (Miller 1938; Spoehr 1926). The increased respiratory rate in host tissues that are infected with powdery mildews may also be of considerable importance in this connection. Yarwood (1934b) reported an increase of 41 per cent in the respiration of clover leaflets infected with mildew, and Pratt (1938), Allen and Goddard (1938), and Allen (1942) found increases of from 250 to 650 per cent in the respiration of wheat infected with *Erysiphe graminis tritici*. Such studies have not been made at a series of temperatures, but one might expect less acceleration of the respiration at the lower temperature, and a consequent conservation of the respiratory substrate which is presumably essential also for the growth of the mildew. Allen's observations (1942) on damage to the photosynthetic mechanism and on changes in soluble sugar content in infected plants also are in accord with the suggestion made above.

Comparative Development of Mildew on Living Plants in Light and in Darkness. It seemed desirable to determine how far development of the mildew might proceed on the living host in darkness. Accordingly, ten pots of wheat plants previously in darkness 24 hours were inoculated. They were then divided into five pairs and one pot of each pair was kept in darkness and one was exposed to twelve hours of illumination daily, at each of five different temperatures. At regular intervals leaves were fixed and bleached in alcohol, cleared in a saturated solution of chloral hydrate, and subsequently mounted in lacto-phenol-aniline blue for microscopical examination. The cycle of powdery mildew development from conidium germination to conidium formation was arbitrarily divided into ten stages that could be easily and unmistakably recognized under the microscope. From table 2 it is easy to determine the stage of development attained in either

TABLE 2. *Effect of temperature upon rate of development of powdery mildew on Marquis wheat in light and in darkness*

Figures are times in hours

Stage of development	10° C		15° C		20° C		25° C		30° C	
	Dark	Light	Dark	Light	Dark	Light	Dark	Light	Dark	Light
1. Germination of conidia	12 (few) 24 (many) 48 (many)	12 (few) 24 (many) 48 (many)	12	12	12	12	12	12	Very sparse after 12 hrs. Spores appear coagulated	
2. Penetration of host epidermis	24–48	24–48	24	24	24	24	24	24	.....	1 case found after 24 hrs.
3. Haustorium initial formed	72	72	24 (?) 48	24 (?) 48	24	24	24	24	.....	.....
4. Haustorium fingers formed	96 (?)	72–96	48 (?)	48	48	48	48	48	.....	.....
5. Superficial mycelium sparse	(?)	96 very sparse	72–96 (very few patches)	72	48	48	48	48	.....	.....
6. Haustorium fingers elongated	120–144	120	72–96 (very few)	72	72	72	72	72	.....	.....
7. Superficial mycelium moderately abundant	.....	144	.....	96	96	72	.....	72	.....	.....
8. Superficial mycelium abundant	.....	192	.....	120	.....	96	.....	96	.....	.....
9. Conidiophores forming	.....	216	.....	120	120 (?)	72–96	120 (???)	96	.....	.....
10. Conidia present	.....	216	.....	120	.....	72–96	.....	96	.....	.....

light or darkness in a given time under the experimental conditions used. The data in table 2 refer to stages of development as seen microscopically and no reference is made here to the relative virulence of the mildew infection at different temperatures. Although in no case was the fungus able to complete its cycle by producing conidia when kept continuously in the dark, it should be noted that for the first two to three days after inoculation development of the mildew proceeded at approximately the same rate in both the light and the dark. Sufficient carbohydrate reserves probably were available in the host to satisfy the requirements of the mold during this period but became depleted in the absence of light before development could be completed. Although conidia were never formed in darkness, conidiophores began to form from the rather meager vegetative mycelium on a few plants at 20° C and 25° C. At those temperatures the rate of development was the same in light and darkness up to the stage at which the superficial mycelium commences to spread. At that point development of the fungus in darkness was checked, however. At lower temperatures—i.e., 10° C and 15° C—development was arrested at an earlier stage. At 30° C germination was poor and no further development occurred. Spores that had been on leaves at 30° C for twelve hours had the same granular and coagulated appearance mentioned previously (Pratt 1943) as characteristic of spores in hanging drops at 35° C. It should be emphasized that the figures in table 2 are merely approximations and represent the time at which the particular stage described appeared to be the most common one to be seen.

TABLE 3. *Effect of quality of radiant energy upon germination of spores of Erysiphe graminis tritici in tap water at 20° C.*

Region of spectrum	Radiant energy (ergs/mm.²/sec.)	Percentage germination
Ultra-violet	6.04	49.7
Blue	6.20	76.1
Green-yellow	6.37	54.5
Short red	6.37	55.1
Long red	6.37	52.6
White light (From Mazda lamp)	8.8	54.8
Control in darkness	.....	71.9

Effect of Light on Germination of Spores. Table 3 shows the results obtained when different sets of mildew spores were germinated on tap water at 20° C for eight hours in darkness and in different regions of the spectrum. All viable spores germinated within eight hours under the conditions of these experiments (see solid curve in figure 1). The relative distribution of the energy values from the different light sources is shown in figure 2, the legend of which also indicates the source of light for each of the wave lengths employed. In each germination test at least 1500 spores

were counted, a sufficiently large number to yield reliable results. All but one of the wave lengths of light that were studied partially suppressed spore germination. Truly critical evaluation and interpretation of the data

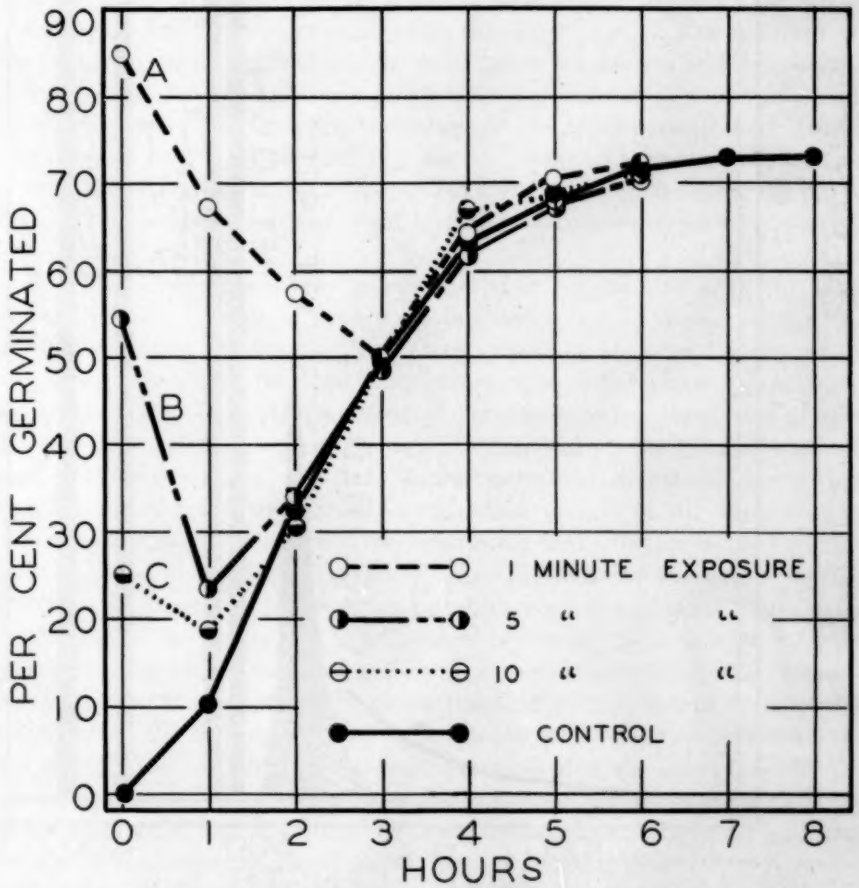

FIG. 1. The solid curve represents the percentage germination of normal *Erysiphe* spores at hourly intervals. Curves A, B, and C represent the percentage of the spores that were germinated after twenty-four hours when the cultures were irradiated for one, five, and ten minutes, respectively, with ultra-violet radiation (principally 365 μ) after immersion in water for the number of hours indicated on the abscissa. (See text for further explanation.)

in table 3 are impossible without more knowledge than is now available of the mildew spores and the compounds of which they are composed. It may be suggested tentatively, however, since no significant effect was noted in the blue light (436 μ), that one or more compounds present in the spores has its minimum absorption (which may be zero) at that wave length and

that the absorption increases as the wave length deviates each way from 436 μ. Further speculation at this time is not warranted by the data, but

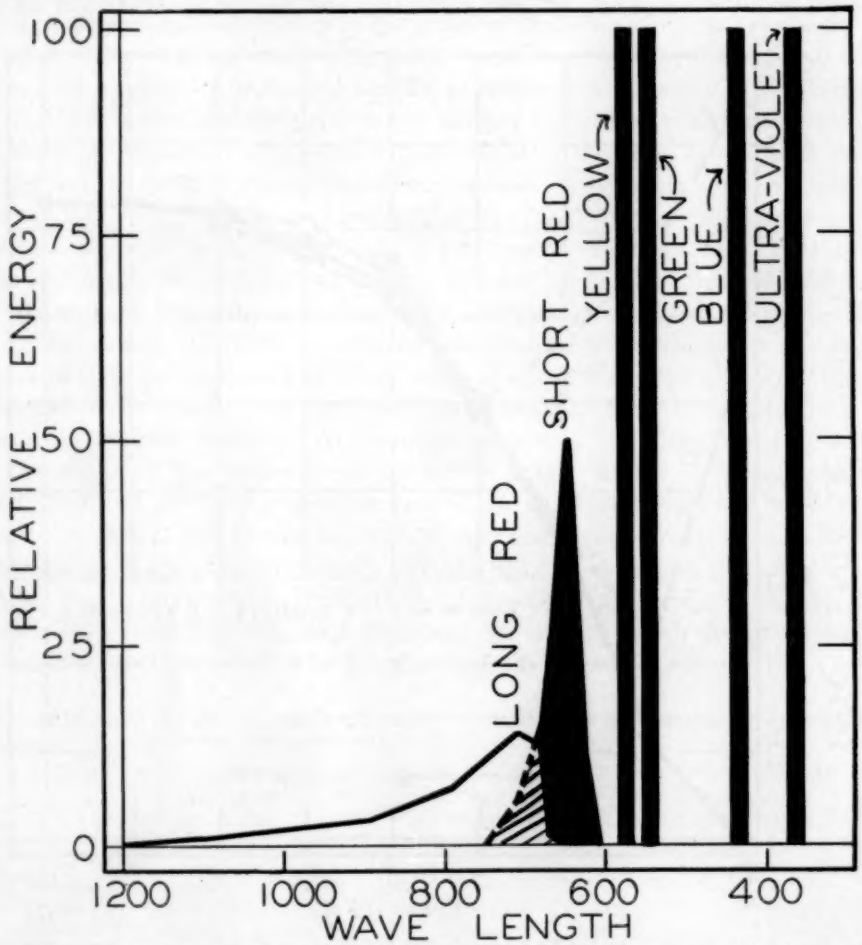

FIG. 2. Distribution of the energy emitted by the different filter combinations and light sources in selected regions of the spectrum. The different points on each curve were obtained by multiplying together the filter transmissions and the radiation values of the sources at the given wave lengths and adjusting the areas under the curves to equivalent values. The source and filter combinations used were as follows: *long-red*–1000 watt lamp, Schott glass filters No. RG 5 (2 mm.) + VG 3 (1 mm.) + H_2O, 5 cm.; *short-red*–1000 watt lamp, Corning filter No. 243 + copper sulphate, 1.2 per cent solution 5 cm. deep + H_2O, 5 cm.; *yellow-green*–quartz mercury arc, tartrazine in gelatine filter + quinine hydrochloride, 0.4 per cent solution 5 cm. deep + copper sulphate, 10 per cent solution 2 cm. deep (this combination gave about equal transmission of the yellow and green lines); *blue*–quartz mercury arc, crystal violet in cellophane filter + quinine hydrochloride, 0.4 per cent solution 5 cm. deep + copper sulphate, 20 per cent solution 2.5 cm. deep; *ultra-violet*–quartz mercury arc, Corning filter No. 586 + copper sulphate, 3 per cent 1 cm. deep. Wave lengths are in millimicrons.

it may be noted in passing that several biological compounds, including some enzymes, are known to possess such characteristics (Miller 1939).

Figure 1 actually represents two graphs, one superimposed upon the other. It shows the percentage germination of *Erysiphe* spores on tap water at successive hourly intervals and also the sensitivity of *Erysiphe* spores to ultra-violet radiation (365 μ). The solid curve is a control and first should be considered alone and entirely apart from the other curves in the figure. It represents the percentage germination of the mildew conidia at hourly intervals on hanging drops of tap water. Since maximum germination (approximately 75 per cent) of the spores occurred in eight hours, the curve was not extended beyond that point although the observations were carried out for 24 hours.

Now the other curves may be considered in conjunction with the solid curve. Different groups of spores on tap water were exposed to the unshielded radiation from a four-inch quartz mercury arc at a distance of 32 cm. for periods of one, five, and ten minutes, after different periods of soaking in water. Thus one set consisting of three groups was irradiated at zero time; another set of three groups was irradiated after one hour of soaking, another after two hours, *et cetera*. Spores were in darkness the entire time they were not being irradiated. Germination counts of all experimental cultures were made 24 hours after irradiation and are represented by the points plotted in curves A, B, and C. The ordinates for the points plotted in curves A, B, and C indicate the percentage germination 24 hours after irradiation of the drops and the abscissas represent the length of time the spores were immersed in water before they were irradiated. Since the solid curve represents the percentage germination of normal spores at the times indicated on the abscissa, it also indicates the percentage of spores in the experimental cultures that had already germinated at the times the different sets of drops were irradiated. Thus at each point the vertical distance between a curve for any irradiated culture (broken line A, B, or C) and that for the control culture (solid curve) represents the percentage of spores in that experimental set which germinated after irradiation. Although only 74.8 per cent of the control spores germinated in 24 hours, 85.3 per cent of those irradiated for one minute at the time of mounting the preparation (zero time) germinated in the same length of time. Maneval (1927) found that the teliospores of each of thirty species of rusts required definite rest periods for physiological maturation before germination could occur and it seems possible that the ultra-violet radiation in these experiments caused an artificial maturation of some sort, as has been described for the fruits of some higher plants, thus rendering about 10 per cent more of the conidia viable. Longer exposures to the radiation were injurious from the start. After the spores had become more hydrated, even the short exposure was

detrimental to them. The injury increased as more water was taken up, so that after three hours of soaking all viable but ungerminated spores were killed by exposure for one minute to radiation from this source. All viable but ungerminated spores were killed by exposure for five minutes or more after two hours of soaking. The suggestion may be offered that increased sensitivity after hydration of the spores was due to an alteration of the molecular configuration of their constituents and that this alteration tended to increase the absorption at the 365 μ wave length. Similar phenomena were not observed at the other wave lengths that were studied.

It is considered that the principal new contributions of the present work are the microscopical observations on the rate and comparative degrees of development of the powdery mildew infection on wheat leaves in the light and in the dark and the observations on the influence of ultra-violet and other radiation on the mildew spores.

SUMMARY

A study was made of the effect of the length of daily period of illumination upon the infection of wheat (*Triticum vulgare*) by the powdery mildew, *Erysiphe graminis tritici*. The influence of irradiation from several different regions of the spectrum upon germination of *Erysiphe* spores was also observed.

Infection of wheat occurred when the plants were illuminated for as little as one hour each day, although the virulence of the infection was somewhat reduced. A three-hour daily period of illumination, however, permitted development of heavy infection. In total darkness, the spores of the parasite germinated and the young mycelia penetrated the host tissue, but the fungus died before sufficient growth occurred for it to become visible macroscopically.

It was found that the blue light (wave length 436 μ) with intensity of 6.2 ergs/mm.^{2}/sec. exerted no effect upon the germination of *Erysiphe* spores. All other regions of the spectrum that were studied at a similar energy value seemed to cause an appreciable reduction in the percentage of spores that germinated in tap water. The spores were highly sensitive to the ultra-violet radiation from a quartz mercury arc and their sensitivity increased as they became more hydrated.

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BULLETIN OF THE TORREY BOTANICAL CLUB

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THE RANDOMNESS OF CHROMOSOME DISTRIBUTION AT ANAPHASE I IN AUTOTRIPLOID LOLIUM PERENNE L.[1]

W. M. MYERS[2]

It has been assumed generally that the third set of chromosomes of triploids is distributed at random during meiosis except for the loss due to lagging. Consequently, it is expected that gametes will be produced with chromosome numbers ranging from haploid to diploid in an approximately binomial frequency (Darlington 1937). This hypothesis has been tested with adequate data in only one species. Satina and Blakeslee (1937a) determined the chromosome assortment in the first division of meiosis in 1,000 pollen mother cells of triploid *Datura stramonium*. When compared with the frequencies expected on the basis of binomial distribution of extra chromosomes from the trivalents, they found an excess of the assortments from 12–24 to 15–21, inclusive, and a deficiency of the 17–19 and 18–18 assortments. Furthermore, the deviations of observed from expected were so great as to leave no question of their statistical significance. In a smaller sample of macrospore mother cells of triploid *Datura*, these authors (1937b) found a similar deviation of observed assortments from expected. On the basis of their results, Satina and Blakeslee (1937a) concluded, "Despite the lack of direct evidence from other forms than *Datura*, it seems probable that the divergence of the assortments at the I division in P.M.C. from calculated values is of general occurrence and is to be attributed to the nature of chromosomes and the mechanisms involved in their movements at division."

The concept of random assortment of the extra chromosomes in triploids and the discrepancies found by Satina and Blakeslee (1937a, b) are of such importance in an understanding of chromosomal behavior during meiosis that it seems imperative that the hypothesis be tested in triploids of other forms. Meiotic behavior of an autotriploid plant of *Lolium perenne* L. was reported by Myers (1943), but at that time too few data were available from anaphase I to provide a critical test of the hypothesis. The triploid plant studied previously was lost, but two more were obtained from crosses of autotetraploid with diploid plants. The present investigation deals with the occurrence and position of univalents at metaphase I and the chromosome numbers in the daughter groups at anaphase I in these two plants.

[1] Contribution No. 55, of the U. S. Regional Pasture Research Laboratory, Divison of Forage Crops and Diseases, Bureau of Plant Industry, Soils, and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture, State College, Pennsylvania, in cooperation with the northeastern states. Assistance in the publication of the tables was obtained from the Lucien M. Underwood Memorial Fund.

[2] Geneticist.

MATERIALS AND METHODS

The two triploid plants were grown in pots in the greenhouse during the winter of 1942–1943. Flowering was induced by use of supplementary illumination to provide a 16-hour daily light period. The microsporocyte material was fixed in acetic alcohol and was examined as soon as possible, all determinations being made within a few days following fixation. All data were taken and the photomicrographs were made from fresh aceto-carmine smear slides. Material was collected from one plant on four different dates. Metaphase I data were taken from only one collection, but anaphase I distributions were counted in all four. Since the chromosomes were not well spread at anaphase I in the second plant and accurate counts were obtained with difficulty, only one collection was made from this plant.

Data were recorded only for anaphase I sporocytes in which both chromosome groups could be counted with certainty. In this manner, the greater ease of counting groups with low numbers was balanced by the correspondingly greater difficulty of counting those with higher numbers.

EXPERIMENTAL RESULTS

Univalents at Metaphase I. Univalent chromosomes at metaphase I are more common in triploid *Lolium perenne* (Myers 1943) than in triploid

TABLE 1. *Number and percentage of metaphase I sporocytes with various numbers and positions of oriented and unoriented univalents*

	Frequency of metaphase I sporocytes showing indicated arrangement of unoriented univalents									
	0	0–1	1–1	0–2	1–2	0–3	2–2	1–3	0–4	Sub total
No oriented univalents										
No.	402	587	226	266	125	61	15	28	10	1720
Per cent	16.1	23.5	9.1	10.7	5.0	2.4	0.6	1.1	0.4	69.0
One oriented univalent										
No.	200	191	60	62	27	7	.....	.....	.....	547
Per cent	8.0	7.7	2.4	2.5	1.1	0.3	.....	.....	.....	21.9
Two oriented univalents										
No.	96	51	14	14	.....	.....	.....	.....	.....	175
Per cent	3.8	2.0	0.6	0.6	.....	.....	.....	.....	.....	7.0
Three oriented univalents										
No.	15	7	.....	.....	.....	.....	.....	.....	.....	22
Per cent	0.6	0.3	.....	.....	.....	.....	.....	.....	.....	0.9
Four oriented univalents										
No.	4	.....	.....	.....	.....	.....	.....	.....	.....	4
Per cent	0.2	.....	.....	.....	.....	.....	.....	.....	.....	0.2
								Grand Total		2494[a] 100.0

[a] Includes 26 sporocytes (1.0 per cent) with five univalents.

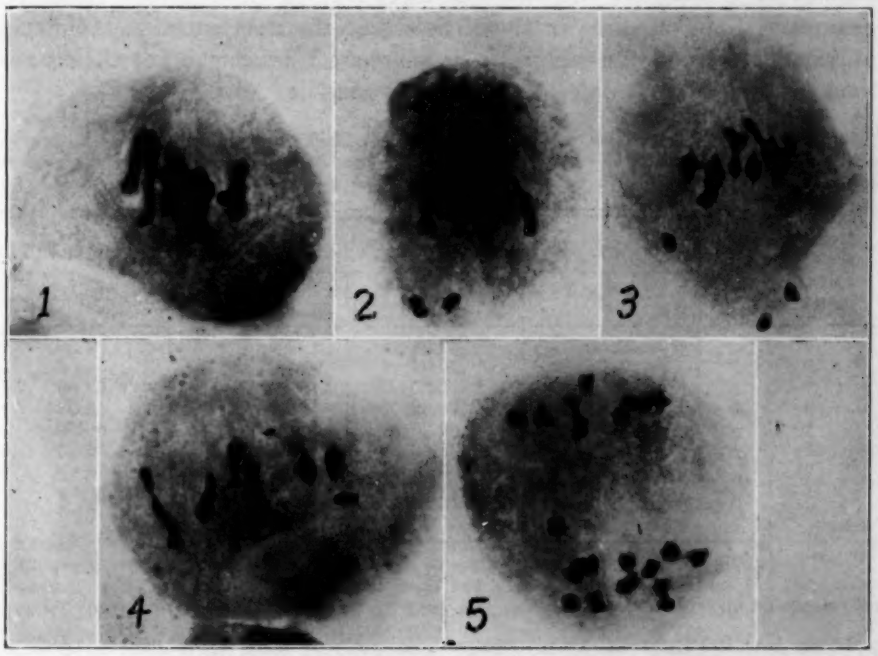
Datura stramonium (Satina and Blakeslee 1937a). Since, as will be shown later, the position of the metaphase I univalents may influence the distribution at anaphase I, this factor is of considerable importance. A total of 2,494 metaphase I sporocytes was recorded (table 1). Sixteen per cent had only trivalents; the remainder had one or more univalents, with a maximum of five observed in 1 per cent of the cells. In 69 per cent of the cells (including the 16 per cent without univalents), there were no univalents oriented on the equatorial plate with the bivalents and trivalents, while there was one oriented univalent (fig. 1) in 22 per cent of the cells, two in 7 per cent, three in 0.9 per cent, and four in 0.2 per cent.

Univalents oriented in this manner at metaphase I would almost certainly lag and divide equationally at anaphase I. Such oriented univalents do not account, however, for all of the anaphase I laggards. There were 69 per cent of the metaphase I sporocytes without oriented univalents, but only 43 per cent of 1,636 anaphase I cells without lagging and equationally dividing chromosomes. Similar comparisons for one, two, three, and four oriented univalents at metaphase I and laggards at anaphase I, respectively, were 22 per cent and 31 per cent; 7 per cent and 18 per cent; 0.9 per cent and 7 per cent; 0.2 per cent and 1.4 per cent. No doubt some of the univalents which were near the equatorial plate but recorded as not oriented would have been oriented at a slightly later stage of metaphase I or at early anaphase I. Also, some of the excess of laggards probably arose from the disjunction of trivalents in the manner described by Darlington (1929, 1937) and Myers (1943).

The univalents that were not oriented on the equatorial plate were found in positions ranging from near the main group of chromosomes to near the poles. Where two such univalents occurred in the sporocytes having no oriented univalents they were found to lie on the same side of the equatorial plate (0–2 position) in 266 sporocytes (fig. 2), and one on each side (1–1 position) in 226 sporocytes. The fit of the observed ratio to the expected 1:1 was satisfactory as shown by X^2 ($0.10 > P > 0.05$). It is apparent (table 1) that the 1–1 and 0–2 positions likewise occurred in approximately equal frequencies in the sporocytes with one and with two oriented univalents. With three unoriented univalents the 1–2 and 0–3 (fig. 3) positions are expected in a 3:1 ratio. Among the sporocytes without oriented univalents, the distribution of these two types deviated significantly from expected (X^2 gave $0.02 > P > 0.01$). On the other hand, the fit to a 3:1 ratio was good for the sporocytes with a single laggard. In cells with four unoriented chromosomes, positions 2–2, 1–3, and 0–4 (fig. 4) are expected in a 3:4:1 ratio and the fit of observed to calculated was satisfactory when tested by X^2 ($0.30 > P > 0.20$).

The results indicate that in general the unoriented metaphase I univalents occur on either side of the equatorial plate at random.

Influence of Metaphase I Univalents upon Distributions Expected at Anaphase I. The influence of the position of unoriented metaphase I univalents upon expected frequencies of various anaphase I distributions is shown in table 2. At anaphase I in this material, no group was observed with less than seven chromosomes. It is probable that one chromosome from each bivalent and trivalent almost invariably moves to each pole at anaphase I. The third chromosome of the trivalents might be expected to pass to either



Metaphase I and anaphase I of meiosis in triploid *Lolium perenne*. Ca 840×. FIG. 1. Metaphase I with one oriented univalent. FIG. 2. Two unoriented univalents in 0–2 position at metaphase I. FIG 3. Three unoriented univalents in 0–3 position at metaphase I. FIG. 4. Four unoriented univalents in 0–4 position at metaphase I. FIG. 5. Anaphase I with one lagging and dividing univalent and a 9–11 chromosome distribution.

pole strictly at random, in which case the distribution of the extra seven chromosomes may be calculated from $(\frac{1}{2}+\frac{1}{2})^7$ (table 2). In sporocytes with one unoriented univalent the distribution likewise should fit the binomial $(\frac{1}{2}+\frac{1}{2})^7$ if it is assumed that the position of the univalent is independent of the distribution of extra chromosomes from the trivalents. When there are two univalents, both unoriented, the expected distribution differs appreciably from the binomial $(\frac{1}{2}+\frac{1}{2})^7$, whether the position of the univalents is 1–1 or 0–2 (table 2). If, on the other hand, these two positions occur with equal frequency, the average of their anaphase I assortments will be exactly like that expected from the random distribution of seven chromo-

somes. A similar situation obtains for three unoriented univalents, the expected average anaphase I assortments fitting the binomial $(\frac{1}{2}+\frac{1}{2})^7$ if the 1–2 and 0–3 positions of the univalents occur in a 3:1 ratio. The same average of anaphase I distributions is expected from sporocytes with four unoriented univalents if the 2–2, 1–3, and 0–4 positions occur in a 3:4:1 ratio.

There may be calculated also the expected ratios of anaphase I distributions when there are one, two, and three lagging chromosomes (oriented metaphase I univalents). In these cases, too, the unoriented metaphase I univalents will not affect the ratio of anaphase I assortments if their positions relative to the equatorial plate are at random.

TABLE 2. *Frequencies of different anaphase I distributions, calculated on the assumption of random disjunction of third chromosome of trivalents, expected from metaphase I sporocytes with no oriented and various numbers of unoriented univalents.*

Number and position of univalents at metaphase I	Percentage of sporocytes with indicated distribution of anaphase I			
	7 – 14	8 – 13	9 – 12	10 – 11
0	1.56	10.94	32.81	54.69
0–1[a]	1.56	10.94	32.81	54.69
1–1	0	6.25	31.25	62.50
0–2	3.12	15.62	34.38	46.88
1–2	0	6.25	31.25	62.50
0–3	6.25	25.00	37.50	31.25
2–2	0	0	25.00	75.00
1–3	0	12.50	37.50	50.00
0–4	12.50	37.50	37.50	12.50

[a] The position of the univalents relative to the equatorial plate. 0–1 indicates a single univalent, 1–1 indicates two univalents, one on each side of the plate, 0–2 indicates two univalents on one side, etc.

The calculations for table 2 and comparisons with univalent positions shown in table 1 are based on the premise that oriented metaphase I univalents lagged at anaphase I while unoriented univalents were included in the daughter chromosome group at the pole near which they lay. It was shown from comparisons of frequencies of oriented univalents and anaphase I laggards that some of the unoriented univalents probably later became oriented and lagged at anaphase I. This might be expected to occur at random so that the relative frequencies of complementary types, i.e., 1–1 with 0–2 positions, etc., will remain unchanged. Since the data presented in table 1 indicated a general tendency for the unoriented univalents to lie on either side of the equatorial plate at random (relative to other univalents), it appears legitimate to calculate the frequencies of different anaphase I assortments by the expansion of $(\frac{1}{2}+\frac{1}{2})^7$ for sporocytes without laggards, $(\frac{1}{2}+\frac{1}{2})^6$ for sporocytes with one laggard, $(\frac{1}{2}+\frac{1}{2})^5$ for sporocytes with two laggards, and $(\frac{1}{2}+\frac{1}{2})^4$ for sporocytes with three laggards.

Chromosome Assortment at Anaphase I. In the four collections from plant 2, counts of chromosome numbers were obtained from a total of 641 anaphase I sporocytes without laggards (table 3). The fit of the total observed ratio to expected on the basis of random assortment was satisfactory as indicated by the X^2 test ($0.20 > P > 0.10$). Values of $P > 0.05$ also were obtained for the data from collections 1 and 3 from this plant but with the data from collections 2 and 4, the deviations of observed from calculated

TABLE 3. *Observed and calculated numbers of four types of anaphase I distributions in sporocytes without lagging chromosomes.*

Source of data		Number of anaphase I with indicated distribution					X^2 for	
		7–14	8–13	9–12	10–11	Total	3 D/F	2 D/F[a]
Plant 2, Coll. 1	Obs.	1	15	41	102	159	.....	.....
	Cal.	2.5	17.4	52.2	87.0	159	6.208	5.751
Coll. 2	Obs.	9	21	65	127	222	.....	.....
	Cal.	3.5	24.3	72.8	121.4	222	10.358	1.284
Coll. 3	Obs.	2	23	69	116	210	.....	.....
	Cal.	3.3	23.0	68.9	114.8	210	0.512	0.072
Coll. 4	Obs.	3	2	21	24	50	.....	.....
	Cal.	0.8	5.5	16.4	27.3	50	10.217	1.948
Total[b]	Obs.	15	61	196	369	641	.....	.....
	Cal.	10.0	70.1	210.3	350.6	641	5.606	2.160
Total of Plant 2	Obs.	15	70	216	401	702	.....	.....
Plus Plant 1	Cal.	11.0	76.8	230.3	383.9	702	3.733	.....

[a] Combining the 7–14 and 8–13 classes.

[b] For plant 2, using four classes, total $X^2 = 27.295$ (12 D/F) and X^2 for heterogeneity $= 21.689$ (9 D/F). Combining the 7–14 and 8–13 classes, total $X^2 = 9.055$ (8 D/F) and $X_h^2 = 6.895$ (6 D/F).

exceeded the conventional level of significance ($0.02 > P > 0.01$). Total X^2 and X^2 for heterogeneity for this plant likewise exceeded X^2 for P of 0.01. It is apparent from examination of the data from collections 2 and 4 that the deviations in the 7–14 class are the principal contributors to the high values of X^2. The difficulty arises from using X^2 when the calculated numbers are small (Fisher 1936). When the data for the 7–14 and 8–13 classes were combined, the fit of observed to calculated was satisfactory as indicated by X^2 for each collection, X^2 for total, total X^2, and X^2 for heterogeneity (table 3). When the data for plant 1 were combined with those for plant 2 (table 3), there was a total of 702 sporocytes. The fit of the observed ratio to calculated was good ($0.30 > P > 0.20$).

In addition to sporocytes without laggards, data were obtained from 501 anaphase I cells with one laggard (fig. 5), 293 with two, 117 with three, and 23 with four. The values of X^2 for the data from the four collections of plant 2 for the sporocytes with one, two, and three laggards are summarized in table 4. All values of total X^2, X_t^2, and X_n^2 gave $P > 0.05$ either when

all classes were used or when the two classes with low calculated frequencies were combined. The fit of observed to calculated also was good in each of the three types of spor· ·tes when the data from plant 1 were combined with data from plant 2. For sporocytes with one laggard $0.30 > P > 0.20$, for those with two laggards $0.95 > P > 0.90$, and for those with three laggards $0.50 > P > 0.30$.

TABLE 4. *Summary of degrees of freedom and values of total X^2, X^2 for total, and X^2 for heterogeneity obtained from data on anaphase I distribution from four collections of plant 2 for sporocytes with one, two, and three lagging chromosomes.*

Number of classes used	Source of X^2	Value of X^2 for sporocytes with indicated number of laggards					
		One		Two		Three	
		D/F	X^2[b]	D/F	X^2[b]	D/F	X^2[b]
All	Total X^2	12	16.017	8	3.605	8	2.761
	X^2 for total	3	3.300	2	0.270	2	0.127
	X^2 for heterogeneity	9	12.717	6	3.335	6	2.634
Combining two classes[a]	Total X^2	8	7.821	4	0.688	4	1.677
	X^2 for total	2	3.258	1	0.166	1	0.007
	X^2 for heterogeneity	6	4.563	3	0.522	3	1.670

[a] 7–13 and 8–12 classes for sporocytes with one laggard, 7–12 and 8–11 classes for those with two laggards, and 7–11 and 8–10 classes for those with three laggards.
[b] All values of X^2 give $P > 0.10$.

DISCUSSION

The results from metaphase I of triploid *Lolium perenne* are consistent in general with the assumption that the unoriented univalents lie in the microsporocyte at random relative to one another and to the equatorial plate. The single exception was in the sporocytes with three univalents, all unoriented, in which the observed ratio of 1–2 and 0–3 positions deviated from the expected 3 : 1 by an amount greater than could be attributed to chance more than one or two times in a hundred. Since all other results were consistent with the hypothesis, it seems probable, nevertheless, that the deviation in this one instance may have been due to chance.

The distributions at anaphase I also were consistent with the hypothesis of chance position of the unoriented metaphase I univalents and random assortment of the extra chromosomes of the trivalents. Thus the results from *Lolium perenne* are contrary to those obtained by Satina and Blakeslee (1937a) from triploid *Datura stramonium*. Rather large samples of sporocytes were used in both experiments and, as pointed out by Satina and Blakeslee (1937a), the chances for systematic errors in observation affecting the results obtained seem to be small. Furthermore, the consistency of results within both species seems to rule out the possibility that the differences in

results are due to chance. It is apparent that the assortment of extra chromosomes at anaphase I in *L. perenne* is not like that in *D. stramonium*. It may be questioned, therefore, whether the unexpected behavior in *Datura* may be attributed, as the authors suggested (1937a), to the general nature of chromosomes and the mechanisms involved in their movements at division. Data from other species besides *Datura* and *Lolium* are required before the general problem of assortment of extra chromosomes can be evaluated properly.

SUMMARY

The occurrence and position of univalents at metaphase I and the assortment of chromosomes at anaphase I were studied in microsporocytes from two autotriploid plants of *Lolium perenne* L. In 84 per cent of 2,494 metaphase I sporocytes, from one to five univalents were found. Of these univalents there was one oriented on the equatorial plate in 22 per cent of the sporocytes, two oriented in 7 per cent, three in 0.9 per cent, and four in 0.2 per cent. In sporocytes with two or more unoriented univalents, the univalents lay in the sporocyte at random relative to one another and to the equatorial plate.

The distribution of chromosomes in 1,636 anaphase I sporocytes was consistent with the assumption of chance position of the metaphase I univalents and random assortment of the extra chromosomes of the trivalents. The behavior in triploid *Lolium perenne* differs from that found in triploid *Datura stramonium* by Satina and Blakeslee (1937a, b).

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STUDIES IN ONAGRACEAE—XIII.[1] THE AMERICAN SPECIES OF LUDWIGIA

PHILIP A. MUNZ

It is a pleasure to acknowledge indebtedness to those in charge of the herbaria listed below and to thank them for their kindness in loan of material used in the preparation of this paper: Field Museum, Chicago, Ill. (FM) for special material; Gray Herbarium of Harvard University (GH); New York Botanical Garden (NY); Pomona College (POM); United States National Herbarium (US) for special material.

It is my regret that in this country we do not have ample material of Ludwigia from the Old World to warrant my including a treatment of the species occurring there, but under the present world conditions it is impossible to borrow such material.

THE GENUS LUDWIGIA[2]

Flowers normally 4-merous, the stamens as many as the sepals and with relatively short filaments. Petals often small or lacking; if conspicuous usually early deciduous. Hypanthium not prolonged beyond the ovary; sepals persistent. Summit of ovary truncate or flattish, or crowned with pyramidal to depressed persistent 4-lobed base of style (stylopodium); style short; stigma capitate to somewhat 4-lobed. Capsule subspheric, to obpyramidal, to elongate and angled or subterete, dehiscing by a terminal pore or longitudinally. Seeds numerous, naked with evident raphe and multiseriate in each cell, or rarely enclosed in endocarp and uniseriate. Mostly perennial swamp-plants, with opposite or alternate leaves and solitary axillary flowers or these in terminal spikes or heads.

TYPE SPECIES: *L. alternifolia* L. A genus of about 30 species, largely American, but with a few in the warmer regions of the Old World. Named for C. G. Ludwig (1709–1773), professor in Leipzig. Among the Old World species may be cited:

(1) *L. palustris*, common to both Old and New Worlds.

(2) *L. ovalis* Miq. from Japan; of the sect. Dantia.

(3) *L. parviflora* Roxb. of Asia and Africa; it may well be a synonym of *L. perennis* L. 1753, a much earlier name. It surely is the same as *Jussiaea caryophyllea* Lam. 1789. It very much resembles *J. erecta*.

(4) *L. prostrata* Roxb. 1820, for which *L. jussiaeoides* Desr. in Lam. 1789 is an earlier name. It is near to *Jussiaea linifolia* Vahl in its uniseriate seeds, each inclosed in a spongy almost rhomboid endocarp.

From a study of the above species one might conclude that *Ludwigia* was derived from *Jussiaea*, to which it is closely related in its persistent sepals, bracteoles at base of hypanthium, mostly multiseriate ovules, etc., and from

[1] No. XII of this series was published in Darwiniana 4: 179–284. 1942.

[2] For spelling, see Int. rules of bot. nomen., ed. 3, Art. 71(4). 1935.

which it is largely separated by having 4 instead of 8 stamens. It may well have arisen by the suppression of the inner whorl of stamens and have originated in the Old World, *L. perennis* and *L. jussiaeoides* being primitive. Within the genus are tendencies to suppress petals, shorten the fruit, develop a stylopodium, toward opposite and even verticillate leaves, etc.

Synonymy in the genus being well established and for the sake of space, it is omitted here.

KEY TO AMERICAN SPECIES OF LUDWIGIA

A. Leaves opposite to whorled; flowering stems prostrate, creeping or floating, rooting freely.

B. Petals lacking or minute; leaves petioled. (Sect. *Dantia.*[3])

TYPE SPECIES: *L. palustris* (L.) Ell.

C. Plants definitely pubescent; bracteoles of hypanthium base not evident. 1. *L. spathulata.*

CC. Plants essentially glabrous; bracteoles usually evident under a lens.

D. Hypanthium and capsule with 4 evident longitudinal green bands and with basal bracteoles not more than 1 mm. long or not evident; petals lacking. 2. *L. palustris.*

DD. Hypanthium and capsule lacking green bands, with bracteoles above the base and 1–5 mm. long; petals present but easily shed. 3. *L. natans.*

BB. Petals conspicuous; leaves subsessile. (Sect. *Ludwigiantha.*[4])

TYPE SPECIES: *L. arcuata* Walt.

C. Pedicels usually 15–35 mm. long, exceeding leaves; petals usually 8–10 mm. long, exceeding sepals. So. Car. to Fla. 4. *L. arcuata.*

CC. Pedicels shorter than leaves; petals 1.3–6 mm. long, not exceeding sepals.

D. Leaves opposite. Plants of U. S.

E. Pedicels 5–15 mm. long; sepals 4–6 mm. long. N. J. to So. Car. 5. *L. brevipes.*

EE. Pedicels 1–2 mm. long; sepals 2.5–3 mm. long. R. I. and Conn. 6. *L. lacustris.*

DD. Leaves whorled. Plants of So. Mexico to Panamá. 7. *L. verticillata.*

AA. Leaves alternate; flowering stems erect or ascending.

B. Capsule on a short pedicel and opening by a terminal pore, cubic-spherical; roots fascicled, often fusiform-thickened; stolons lacking. (Sect. *Ludwigiaria.*[5])

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[3] *Dantia*, as sect., DC. Prodr. **3**: 61. 1828; as genus, Petit ex L. Gen. ed. 1, 337. 1737. *Danthia* Steud. Nom. ed. 2, **1**: 482. 1840. *Isnardia* as sect., Torrey & Gray, Fl. N. Am. **1**: 525. 1840; as genus, L. Sp. Pl. 120. 1753. Rather succulent herbs, usually with opposite petioled leaves which are not much reduced up the stems; rooting freely at nodes; stipules minute, triangular, glandlike; flowers minute, solitary in axils; hypanthium oblong-obovoid or turbinate, somewhat 4-sided, with or without basal bracteoles; sepals deltoid; petals present or lacking; capsule more or less corky, septicidal, short, flat at the somewhat 4-lobed apex.

[4] *Ludwigiantha*, as sect., Torrey & Gray, Fl. N. Am. **1**: 526. 1840; as genus, Small, Bull. Torrey Club **24**: 177–178. 1897. Stems prostrate or decumbent, creeping or floating; leaves opposite to whorled, sessile or nearly so, numerous, not much reduced up the stems; flowers solitary in leaf-axils, pedicelled, with pair of setaceous bractlets at base of hypanthium; petals conspicuous, but readily shed; filaments widened toward base; capsules usually curved at base, elongate-clavate, with a prominent 4-lobed stylopodium.

[5] *Ludwigiaria*, as sect., DC. Prodr. **3**: 60. 1828. Sect. *Euludwigia*, Torrey & Gray, Fl. N. Am. **1**: 522. 1840; "*Alternifoliae*" of Small, Man. S.E. Fl. 941. 1933. Roots fascicled, more or less fusiform, perennial; stems erect; leaves alternate; petals well developed; stylopodium hairy; capsules pedicelled, opening by a terminal pore on dehiscence of style.

TYPE SPECIES: *L. alternifolia* L.

C. Plant hirsute; capsules hirsute, shorter than the lance-deltoid sepals which are about 1 cm. long in fruit. 8. *L. hirtella.*

CC. Plant glabrous or puberulent; sepals ovate to lance-ovate.

D. Cauline leaves sessile; petals much longer than sepals; pedicel longer than capsule.

E. Style 7–10 mm. long; leaves glabrous to minutely puberulent under a lens; flowers in axils of bracts less than 1 cm. long. 9. *L. virgata.*

EE. Style 3–5 mm. long; leaves obviously pubescent, usually to naked eye; flowers borne in axils of bracts 1–2.5 cm. long. 10. *L. maritima.*

DD. Cauline leaves with short petioles; petals about as long as sepals; pedicel not longer than capsule. 11. *L. alternifolia.*

BB. Capsule sessile, dehiscing by valves separating from the disk-like top; plants with creeping stolons. (Sect. *Microcarpium.*[6])

C. Capsule about as long as thick, subspherical to cubic-spherical.

D. Cauline leaves not spatulate; capsule mostly 3–5 mm. long.

E. Plant conspicuously pilose; upper leaves subelliptic; flowers somewhat crowded at ends of branches. 12. *L. pilosa.*

EE. Plant glabrous to puberulent to pubescent in upper parts; upper leaves mostly lance-linear.

F. Flowers in terminal heads; bractlets at base of hypanthium ovate to elliptic-lanceolate. 13. *L. suffruticosa.*

FF. Flowers in elongate interrupted leafy spikes; bracteoles mostly more narrow or lacking.

G. Capsules sharply 4-angled or -winged.

H. Seeds cylindric, 3–4 times as long as wide; sepals deltoid-ovate, about as wide as long, shorter than the capsule. 14. *L. lanceolata.*

HH. Seeds ovoid, about twice as long as wide; sepals slightly longer than wide, about as long as capsule. 15. *L. alata.*

GG. Capsules subglobose, scarcely 4-sided.

H. Bracteoles at or just above base of hypanthium, 2–5 mm. long; seeds yellowish. 16. *L. polycarpa.*

HH. Bracteoles if evident less than 1 mm. long; seeds brown. 17. *L. sphaerocarpa.*

DD. Cauline leaves spatulate or nearly so; capsule 1–3 (4) mm. long.

E. Capsule 1–1.5 mm. long, shorter than the broad spreading sepals; leaf-blades usually at least half as wide as long. Car. to La., Bahamas, Cuba. 18. *L. microcarpa.*

EE. Capsule 2–4 mm. long, longer than sepals.

F. Leaf-blades spatulate-obovate to spatulate, 3–7 mm. wide, about 2–3 times as long.

G. Capsule 2–2.5 mm. long; leaf-blades mostly at least half as wide as long. Fla., Cuba, Jamaica. 19. *L. Simpsoni.*

GG. Capsule 3–4.5 mm. long; leaf-blades mostly about one-third as wide as long. Fla. 20. *L. spathulifolia.*

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cubic-spherical, perhaps tardily loculicidal; bracteoles well developed at base of hypanthium; base of stem often with considerable aerenchyma but lacking stolons.

[6] **Microcarpium** Munz, sect. nov. (''*Microcarpeae*'' of Small, Man. S.E. Fl. 941. 1933.) Plantae nostrae fere perennes, cum stolonibus foliosis et postea surculis erectis; foliis alternis; floribus sessilibus axillaribusque, aliquando in spicis aut capitulis confertis; capsula valvis dehiscente, quae ab apice discoideo separant, subspherica aut cubico-spherica aut obpyramidale aut cylindrica. TYPE SPECIES: *L. pilosa* Walt.

FF. Leaf-blades narrow-spatulate, 1–3 (4) mm. wide, at least 4 times as long; capsule 2.5–3.5 mm. long. Fla. 21. *L. Curtissii.*

CC. Capsule definitely longer than thick, cylindric to 4-angled.

D. Petals lacking; bracteoles linear, scarcely 1 mm. long; capsules subcylindric, sometimes slightly 4-grooved. 25. *L. glandulosa.*

DD. Petals equalling or exceeding sepals, but easily shed.

E. Capsules subcylindric, not much thickened upward.

F. Leaves linear, 1–2.5 mm. wide; sepals 4–6 mm. long; capsules 8–9 mm. long. U.S. 22. *L. linifolia.*

FF. Leaves narrow-spatulate, 2–5 mm. wide; sepals 2 mm. long; capsules 5–7 mm. long. Cuba. 23. *L. stricta.*

EE. Capsules 4-angled, about twice as thick at summit as at base. U.S. 24. *L. linearis.*

TREATMENT OF SPECIES

1. LUDWIGIA SPATHULATA Torr. & Gray, Fl. N. Am. **1**: 526. 1840.

Isnardia spathulata Kuntze, Rev. Gen. 1: 251. 1891; Small, Bull. Torrey Club **24**: 177. 1897.

Plant pubescent; stems 1–3 dm. long; leaves rhombic-spatulate to ovate, 1–1.5 (2) cm. long, 3–8 mm. wide, with 4–5 inconspicuous veins on each side of midrib, gradually narrowed into petioles 3–10 mm. long; sepals suborbicular-ovate, 1–1.5 mm. long; petals lacking; capsule globose-obovoid, 3 mm. long.

Type locality: "Middle Florida, *Dr. Chapman.*" *Material seen,* all from Florida: without definite locality, *Chapman* (GH); Gadsden Co., *Chapman in 1835* (NY); Walton Co., De Funiak Springs, *Curtiss 6853* (GH, NY).

2. LUDWIGIA PALUSTRIS (L.) Elliott, Sketch Bot. S. Car. & Ga. **1**: 211. 1821.

Isnardia palustris L. Sp. Pl. 120. 1753.

Nearly or quite glabrous, succulent; leaves lanceolate to elliptic-ovate, the blades 3–25 mm. long, on petioles 3–20 (25) mm. long; flowers sessile, axillary; hypanthium usually with 4 longitudinal green bands; capsule somewhat corky, oblong-obovoid, somewhat 4-sided, rounded at base, truncate at apex, 2–5 mm. long, 1.4–3.5 mm. thick.

The var. *typica* Fernald & Griscom (Rhodora **37**: 176. 1935) is characterized by having the green bands on the hypanthium terminating well below the summit. It occurs in Europe, Africa, and western Asia. The American varieties were recently thoroughly treated by Fernald and Griscom (Rhodora **37**: 176) and for sake of space do not need consideration here. They may be keyed as follows:

A. Leaf-blades usually at least half as wide as long; capsules 2–3.5 mm. thick. Atlantic Coast to Cascade Mts. and Sierra Nevada; occasional to Central America. var. *americana* (DC.) Fern. & Griscom.

AA. Leaf-blades one-third to one-fourth as wide as long.

B. Leaf-blades mostly less than 1 cm. long; capsules less than 2 mm. thick. Southern U.S. to Colombia. var. *nana* Fern. & Griscom.

BB. Leaf-blades mostly more than 1 cm. long; capsules 2–2.8 mm. thick. Brit. Columbia to Calif. west of the mts. var. *pacifica* Fern. & Griscom.

3. LUDWIGIA NATANS Elliott, Sketch Bot. S. Car. & Ga. **1**: 581. 1821.

Much like *L. palustris*, but leaf-blades 5–45 mm. long, 3–30 mm. wide, rhombic-ovate to almost orbicular-ovate or -obovate; flowers sessile or short-pedicelled; hypanthium lacking green bands, and with more evident bractlets; capsule 3–8 mm. long.

Key to Varieties of *L. natans*

A. Fruits 3–5 (6) mm. long, sessile or on pedicels up to 1 mm. long; bracteoles mostly 1–3 mm. long; petioles mostly 3–10 mm. long. Carolina to Missouri, Texas, Cuba, Bermuda. var. *typica* Fern & Griscom.

AA. Fruits 6–8 mm. long; bracteoles mostly 2–5 mm. long; petioles 5–20 mm. long.

B. Fruits sessile, mostly 2–2.5 mm. thick. Atlantic Coast of U.S. to Rocky Mts. and West Indies. var. *rotundata* (Griseb.) Fern. & Griscom.

BB. Fruits on pedicels 2–4 mm. long and mostly 3–3.5 mm. thick. S. Calif. var. *stipitata* Fern. & Griscom.

Since this species was also recently treated by Fernald & Griscom, Rhodora **37**: 175. 1935, I shall omit further discussion here.

4. LUDWIGIA ARCUATA Walt. Fl. Car. 89. 1788.

Isnardia arcuata Kuntze, Rev. Gen. **1**: 251. 1891. *Ludwigiantha arcuata* Small, Bull. Torrey Club **24**: 178. 1897. *Ludwigia pedunculosa* Michx. Fl. Bor. Am. **1**: 88. 1820. *Isnardia pedunculosa* DC. Prodr. **3**: 60. 1828.

Fleshy, subglabrous to strigulose, the creeping stems 5–25 cm. long; leaves rather crowded, the blades oblanceolate to elliptic-linear, 8–20 mm. long, 1–2.5 mm. wide, sessile or nearly so; pedicels 15–35 mm. long; bracteoles 1–3 mm. long; hypanthium elongate-funnelform; sepals linear-lanceolate, spreading, acuminate, 4–8 mm. long; petals 6–10 mm. long; capsule clavate-oblong, somewhat arcuate at base, 6–8 mm. long, 2–3 mm. thick, somewhat 4-sided.

Type locality: Carolina; range from South Carolina to Florida. *Represented by:* S. CAROLINA: Charleston Co., near Charleston, *Ravenel* (GH). GEORGIA: Chatham Co., Savannah, *Canby in 1869* (GH, NY). FLORIDA: Leon Co., Jackson Lake, *Wiegand & Manning 2182* (GH, POM); Jefferson Co., Lloyds, *Nash 2509* (GH, NY); Lake Co., Eustis, *Nash 607* (GH, NY); Hillsborough Co., Tampa, *Curtiss 934* (GH, NY).

5. LUDWIGIA BREVIPES (Long) E. H. Eames, Rhodora **35**: 228. 1933.

Ludwigiantha brevipes Long, in Britton & Brown, Ill. Fl. ed. 2, **2**: 586. 1913.

Leaves 2–6 mm. wide; pedicels 5–15 mm. long; petals 4–6 mm. long; capsule clavate, 7–10 mm. long.

Type locality: Little Egg L. S. S., Long Beach Island, Ocean Co., New Jersey. Ranging south to S. Carolina. *Represented by: Long 173,* type coll. (GH, NY). VIRGINIA: *Fernald & Long 8376* (GH, NY, POM); *Fernald & Long 4070* (GH, NY). N. CAROLINA: *Godfrey 5247* (GH). S. CAROLINA: *Godfrey & Tryon 1195* (GH, NY, POM).

6. LUDWIGIA LACUSTRIS E. H. Eames, Rhodora **35**: 228. 1933.

L. lacustris f. *aquatilis* Eames, Rhodora **35**: 229. 1933.

Like the preceding, but with pedicels 1–2 mm. long; petals 1.3–3 mm. long; capsules about 5 mm. long.

Type locality: Watchaug Pond, Charleston, Washington Co., R. I. Type seen, also collections from CONNECTICUT: New Haven Co., Guilford, *Eames 11473, 11474a, 11475, 11476* (GH); New London Co., Old Lyme, *Eames 11496, 11494, 11495* (GH); Lyme, *Eames 11460* (GH).

7. **Ludwigia verticillata** Munz, sp. nov.

Caules tenues, 1–2 mm. crassi, subglabri, virides, cum ramis decumbentibus aut ascendentibus, 3–15 cm. longis; internodis 2–8 mm. longis; foliis numerosis, verticillatis (3, 4, ad 6), anguste elliptico-oblanceolatis, 8–18 mm. longis, 1–3 mm. latis, in extremis ambobus acutis, subintegris, glabris, cum petiolis 1–2.5 mm. longis, laminis cum 7 venis principalibus in latere quoque; floribus paucis, in axillis superioribus solitariis; pedicellis 1.5–3 mm. longis; bracteolis vix evidentibus; hypanthio glabro, clavato-subcylindrico, in anthese 5–6 mm. longo; sepalis deltoideo-ovatis, 2.5–4 mm. longis, 1.5–2 mm. latis, subobtusis, 3–5-venatis; petalis 4–5 mm. longis et latis; staminibus 1.5–2.5 mm. longis; filamentis base latis; antheris circa 0.7 mm. longis; stylopodio depresso, piloso; stylo crasso, ca. 2 mm. longo; stigmate 1 mm. crasso; capsula glabra, 7–8 mm. longa, 1.5–2 mm. crassa, vix 4-angulata, cum stria mediana in superficie quoque; seminibus in serie una indefinita in loculo quoque, subovoideis, ca. 0.6 mm. longis, ferrugineis, nitidis.

TYPE: Laguna de Portola, near Chepo, province of Panamá, Panamá, at 50 m. alt., *H. Pittier 4605*, Oct., 1911, U. S. Nat. Herb. no. 679760. *Other collections seen:* HONDURAS: Amapala, Isla Tigre, *Standley 20771* (US). MEXICO: "Acapulco and vicinity," *Palmer 577* (US).

In general appearance, elongate fruit, broad filaments and evident petals near to *L. lacustris, L. brevipes,* etc., but distinct in its whorled leaves, seeds seemingly in 1 row, stylopodium less prominent and hairy, reduced bracteoles, and southern range.

8. LUDWIGIA HIRTELLA Raf. Med. Rep. N. Y. **5**: 358. 1808.

Isnardia hirtella Kuntze, Rev. Gen. **1**: 251. 1891. *L. pilosa* Elliott, Sketch Bot. S. Car. & Ga. **1**: 216. 1821, not Walter, 1788. *L. permollis* Barton, Fl. Virg. **1**: 52. 1812, from description. *L. hirsuta* Pursh, Fl. Am. Sept. **1**: 110. 1814, not Desr. 1789. *Isnardia hirsuta* R. & S. var. *permollis* DC. Prodr. **3**: 60. 1828.

Erect, 3–9 dm. high, hairy; leaves sessile, lance-oblong to ovate-oblong, hirsute, 2–5 cm. long, 0.5–1.2 cm. wide, gradually reduced upward; pedicels 3–8 mm. long; bracteoles 3–4.5 mm. long; sepals 7–10 mm. long; petals 10–15 mm. long; capsule subglobose-cubical, hirsute, green at the prominent angles, 4–6 mm. long; seeds 0.6 mm. long.

Type locality: Baltimore, Md. Range along the coast from New Jersey to northern Florida, and eastern Texas. For sake of space citation of specimens is omitted.

9. LUDWIGIA VIRGATA Michx. Fl. Bor. Am. **1**: 89. 1803.

Isnardia virgata DC. Prodr. **3**: 60. 1828.

Stems simple or few-branched, fine-puberulent to glabrous, 3–8 dm. high; leaves sessile, not crowded, lowermost oblong, 1–3 cm. long, principal ones

oblong-lanceolate to oblong-linear, 3–6 (8) cm. long, 3–7 mm. wide, gradually reduced up the stem to oblong-linear bracts 5–8 mm. long; leaves subglabrous to puberulent; flowers in terminal spicate racemes; pedicels 6–10 (15) mm. long; bracteoles 2–5 mm. long; sepals reflexed, 6–11 mm. long, 3.5–4.5 mm. wide, lance-deltoid; petals 10–15 mm. long; style 7–10 mm. long; stigma 2 mm. thick; capsule subglobose-spherical, 5–6 mm. long, almost winged at the sharp angles; seeds light brown, shining, 0.6–0.7 mm. long.

Type locality: S. Carolina. Ranging along the coast from North Carolina to northern Florida. Much material which has been referred here belongs to *L. maritima*. *Representative of L. virgata:* N. CAROLINA: New Hanover Co., Wilmington, *Biltmore Herb. 4168* (GH, NY); Moore Co., Pine Bluff, *Wiegand & Manning 2203* (GH); Columbus Co., Bolton, *Wiegand & Manning 2204* (GH, POM). S. CAROLINA: Williamsburg Co., Kingstree, *Wiegand & Manning 2205* (GH, POM); Salters, *Godfrey & Tryon 523* (GH, NY, POM); Charleston Co., McClennanville, *Godfrey & Tryon 1132* (GH, NY, POM). GEORGIA: Ware Co., Suwanee Lake, *Harper 272* (GH, NY). FLORIDA: Wakulla Co., St. Marks, *Rugel in 1843* (NY); Duval Co., Jacksonville, *Curtiss 919* (GH, NY).

10. LUDWIGIA MARITIMA Harper, Torreya **4**: 163. 1904.

Like the preceding, but more definitely and evidently pubescent throughout, with hairs up to 0.5 mm. long; upper bract-like leaves 1–2.5 cm. long; bracteoles 2–3.5 mm. long; sepals 5–9 mm. long; petals 9–12 mm. long; style 3–5 mm. long; stigma 1–1.5 mm. thick; capsule 6–8 mm. long.

Type locality: Cumberland Island, Camden Co., Ga. In pine lands from coastal N. Carolina to southern Florida and eastern Louisiana. *Representative collections:* N. CAROLINA: Craven Co., *L. F. & F. R. Randolph 549* (GH). S. CAROLINA: Georgetown Co., Georgetown, *Godfrey & Tryon 786* (GH, NY, POM). GEORGIA: Camden Co., Cumberland I., type coll. *Harper 1542* (FM, GH, NY). FLORIDA: Duval Co., Jacksonville, *Curtiss 4912* (GH, NY). Brevard Co., Okeechobee region, *Fredholm 5996* (GH, NY). Lake Co., Eustis, *Nash 750* (GH, NY). Manatee Co., Bradentown, *Tracy 7087* (GH, NY). Dade Co., Cutler, *Small, Mosier & Small 6702* (GH, NY). ALABAMA: Mobile Co., near Mobile, *Munz 13353* in part (POM); *Baker 850* (NY). MISSISSIPPI: Harrison Co., Biloxi, *Baker in 1897* (NY, POM); Jackson Co., Ocean Springs, *Pollard 1112* (GH, NY, POM). LOUISIANA: St. Tammany Parish, Slidell, *Munz 13347* in part (NY, POM), *13346* (POM).

11. LUDWIGIA ALTERNIFOLIA L. Sp. Pl. 118. 1753.

Plant 4–12 dm. tall; leaves rather crowded, with petioles 3–10 mm. long and principal leaf-blades 4–8 (12) cm. long; pedicels 2–5 mm. long; bracteoles 1–2.5 mm. long; sepals 7–10 mm. long; petals 8–10 mm. long; capsule cubic with rounded base, slightly wing-angled, mostly 5–6 mm. long.

11a. L. ALTERNIFOLIA L. var. **typica** Munz, var. nov.

L. alternifolia L. Sp. Pl. 118. 1753. *Isnardia alternifolia* DC. Prodr. 3: 60. 1828. *L. ramosissima* Walt. Fl. Car. 89. 1788? *L. angustifolia* β *ramosissima* Poir. in Lam. Encycl. Suppl. 3: 513. 1813. *L. macrocarpa* Michx. Fl. Bor. Am. 1: 89. 1803. *L. aurantiaca* Raf. Med. Rep. N. Y. 5: 358. 1808? *Isnardia aurantiaca* DC. Prodr. 3: 61. 1828? *Ludwigia uniflora* Raf. Med. Rep. N. Y. 5: 358. 1808? *Isnardia alternifolia* γ *uniflora* DC. Prodr. 3: 60. 1804? *L. salicifolia* Poir. in Lam. Encycl. Suppl. 5: 512. 1813. *Isnardia alternifolia* β *salicifolia* DC. Prodr. 3: 60. 1804. *L. microcarpa* Link, Enum. Hort. Berol. 141. 1821. *Rhexia linearifolia* Poir. in Lam. Encycl. 6: 2. 1804? *Ludwigia alternifolia* var. *linearifolia* Britton, Bull. Torrey Club 17: 315. 1890.

Plant subglabrous or more or less strigulose on stems, pedicels and leaves.

Type locality: "Habitat in Virginia." Very common and ranging from Massachusetts to northern Florida, Ontario, Iowa, and Louisiana. Intergrading with the following variety; some specimens, especially from the southern and western parts of the range becoming more pubescent, although the hairs may be quite appressed.

11b. L. ALTERNIFOLIA L. var. PUBESCENS Palmer & Steyermark, Ann. Mo. Bot. Gard. **25**: 772. 1938.

Stems, leaves, pedicels, and capsules densely pubescent with erect hairs.

Type locality: 4 miles west of Charleston, Mississippi Co., Mo., the TYPE being *Palmer & Steyermark 41450. Other collections seen:* INDIANA: *Deam 41713.* ILLINOIS: *Waite 1177.* KANSAS: *Norton 155, Rydberg & Imler 401.* ARKANSAS: *Demaree 17767, 19907, 20064, 20149, 15612, 19793,* etc, LOUISIANA: *Hale, Drummond, Palmer 8012, Ball 617.* TEXAS: *Wright, Lindheimer 69, Cory 25300.*

12. LUDWIGIA PILOSA Walt. Fl. Car. 89. 1788.

Isnardia pilosa Kuntze, Rev. Gen. 1: 251. 1891. *Ludwigia rudis* Walt. Fl. Car. 89. 1788. *L. hirsuta* Desr. in Lam. Encycl. 3: 614. 1789. *I. hirsuta* R. & S. Syst. 3: 477. 1818, as to name and in part as to concept; DC. Prodr. 3: 60. 1828. *L. mollis* Michx. Fl. Bor. Am. 1: 90. 1803. *I. mollis* Poir. in Lam. Encycl. Suppl. 3: 188. 1813. *L. capitata* var. *pubens* Torr. & Gray, Fl. N. Am. 1: 525. 1840.

Stoloniferous at base, the main stems soon erect, 5–12 dm. high, pilose; leaves of stolons orbicular- to oblong-ovate, with blades 8–16 mm. long, petioles 5–8 mm. long; cauline leaves oblong-lanceolate to elliptic to linear-lanceolate, petioles 1–5 mm. long, blades 2–10 cm. long, reduced up the stem; flowers usually crowded toward ends of branches; bracteoles 3–4 mm. long; sepals 4–5 mm. long; petals apparently lacking; capsules sessile, cubic-globose, somewhat 4-sided but not sharply angled, 3–4 mm. long.

Type locality: Carolina. Range along coast from southern Virginia to Florida and eastern Texas.

13. LUDWIGIA SUFFRUTICOSA Walt. Fl. Car. 90. 1788.

Isnardia suffruticosa Kuntze, Rev. Gen. 1: 251. 1891. *Ludwigia capitata* Michx. Fl. Bor. Am. 1: 90. 1803. *Isnardia capitata* DC. Prodr. 3: 60. 1828.

Stolons pubescent, with almost sessile leaves; main stems glabrous, the main leaves sessile, linear-lanceolate to lanceolate, 3–8 (10) cm. long; flowers in subcapitate spikes; pedicels less than 1 mm. long; bracteoles 3 mm. long; sepals 2.5–3 mm. long; petals not seen; capsule broadly obpyramidal, somewhat quadrangular but rounded at angles, 3.5–4 mm. long, slightly thicker.

Type locality: Carolina. Ranging along coast from N. Car. to south central Fla.

14. LUDWIGIA LANCEOLATA Elliott, Sketch Bot. S. Car. & Ga. 1: 213. 1821.

Isnardia lanceolata DC. Prodr. 3: 61. 1825.

Leaves of stolons elliptic- to rhombic-obovate or narrower, 1.5–3 cm. long, short-petioled; principal cauline leaves oblanceolate to linear-lanceolate, 2–8

(10) cm. long, 2–8 (11) mm. wide, sessile or on petioles a few mm. long; flowers almost sessile, in spikes several cm. long; bracteoles 2–3 mm. long; sepals deltoid-ovate, abruptly acute, 3 mm. long; petals none; capsules obpyramidal, almost winged at the sharp angles, 4–4.5 mm. long, about as thick; seeds cylindric, about 0.7 mm. long, one-third to one-fourth as thick.

Type locality: "swamps of Georgia"; much confused with the next species. *Representative collections:* GEORGIA: swamps, *Baldwin*, type at Elliott Herbarium (photo POM); *Harper 1605* and *1483*. FLORIDA: *Biltmore Distribution 4177, Nash 2502, Rugel 245, Curtiss 927, Fredholm 5987, Small & Carter 2627*.

15. LUDWIGIA ALATA Elliott, Sketch Bot. S. Car. & Ga. **1**: 212. 1821.

Isnardia alata DC. Prodr **3**: 61. 1828. *Ludwigia simulata* Small, Fl. S. E. U. S. 816, 1335. 1903.

Like the preceding, but leaves of stolons perhaps more round; sepals deltoid, about 3 mm. long, connate at very base, abruptly subacuminate, somewhat denticulate; capsule 3–4 mm. long; seeds ovoid, about 0.6 mm. long and half as thick.

Type locality: Sullivan's Island, Charleston Co., S. C. Ranging along coast from southeastern Virginia to Florida and Mississippi. *Representative collections:* VIRGINIA: *Fernald, Long and Fogg 4960*, and *13981* and *13982*. N. CAROLINA: *Lewis 196, Godfrey & Tryon 718*. GEORGIA: *Harper 1554*. FLORIDA: *Rugel in 1843, Curtiss 929, Wiegand & Manning 2172, Hitchcock 113, Small & Carter 1243* and *2624*. MISSISSIPPI: *Lloyd & Tracy 230* and *6415*.

16. LUDWIGIA POLYCARPA Short & Peter, Transylv. Jour. Med. **8**: 581. 1835; ex Torrey & Gray, Fl. N. Am. **1**: 525. 1840.

Isnardia polycarpa Kuntze, Rev. Gen. **1**: 251. 1891.

Leaves on stolons crowded, oblanceolate, 1–2.5 cm. long, those on main stems narrowly lanceolate to oblanceolate, 3–12 cm. long, with winged petioles 2–8 mm. long; flowers sessile; bractlets 2–5 mm. long; sepals 2.5–3.5 mm. long; capsule subglabrous, turbinate, scarcely 4-sided, 3.5–5 mm. long, 3–3.5 mm. thick; seeds yellowish, somewhat punctate under a lens.

Type locality: Kentucky. Moist places, Massachusetts and Connecticut, Ontario to Tennessee and Kansas. Not easily confused with other species.

17. LUDWIGIA SPHAEROCARPA Elliott, Sketch Bot. S. Car. & Ga. **1**: 213. 1821.

Isnardia sphaerocarpa DC. Prodr. **3**: 61. 1828.

Leaves of stolons elliptic-lanceolate to spatulate-obovate, 1–2 cm. long, principal cauline leaves lanceolate to lance-oblong, 2–10 (12) cm. long, 3–8 (10) mm. wide, sessile or with petioles to 7 mm. long; flowers sessile; bracteoles not more than 1 mm. long; sepals 2.5–3 mm. long; capsule subglobose, 2.5–4.5 mm. long, pubescent to glabrous.

Key to varieties of *L. sphaerocarpa*

A. Fruit crowded on branches, 3.5–4.5 mm. long, not so wide. Massachusetts to New Jersey. 17c. var. *macrocarpa.*

AA. Fruit not crowded on branches, 2.5–3.2 mm. long, usually wider.

B. Main stems and leaves usually glabrous; main leaves linear-lanceolate and more than 7 cm. long. R. I. to Fla. 17a. var. *typica.*

BB. Main stems and leaves pubescent to strigose, lanceolate, usually less than 7 cm. long. N. J. to Va., Mich., Ind. 17b. var. *jungens.*

17a. L. SPHAEROCARPA Elliott var. TYPICA Fernald & Griscom, Rhodora **37**: 174. 1935.

Since this and the following varieties were amply discussed in 1935 and many specimens were cited, I shall not repeat the material here.

17b. L. SPHAEROCARPA L. var. JUNGENS Fernald & Griscom, Rhodora **37**: 174. 1935.

L. sphaerocarpa var. *Deamii* Fernald & Griscom, Rhodora 37: 174. 1935.

In my opinion the var. *Deamii* was based on inadequate material; other collections than the type and from the same region do not bear out its characters. Var. *typica* and var. *jungens* intergrade freely.

17c. L. SPHAEROCARPA L. var. MACROCARPA Fernald & Griscom, Rhodora **37**: 174. 1935.

New Jersey material is sometimes difficult to distinguish from var. *typica.*

18. LUDWIGIA MICROCARPA Michx. Fl. Bor. Am. **1**: 88. 1803.

Isnardia microcarpa Poir. in Lam. Encycl. Suppl. 3: 188. 1813. *Ludwigia glandulosa* Pursh, Fl. Am. Sept. 1: 111. 1814, not Walter, 1788.

Creeping at base, the erect stems slender, 1–6 dm. high; leaves of main stems obovate-spatulate to spatulate, 7–25 mm. long, 4–10 mm. wide, with petioles 1–4 mm. long; flowers sessile, solitary; bracteoles 0.5–1.5 mm. long; sepals orbicular-ovate, 1–2 mm. long; petals none; capsule obpyramidal with rounded corners, 1–1.5 mm. long, 1.5–2 mm. thick at summit.

Type locality: South Carolina. Near the coast from N. Carolina to southern Florida and Louisiana; reported also from Tennessee, Missouri, Bahamas, and Cuba. Often difficult to distinguish from some of the following species; *representative material* is cited: NORTH CAROLINA: Carteret Co., Beaufort, *Lewis 197* (NY). So. CAROLINA: Horry Co., Myrtle Beach, *Godfrey & Tryon 1163* (GH, NY, POM); Georgetown Co., near Georgetown, *Godfrey & Tryon 1043* (GH, NY, POM). GEORGIA: Sumter Co., *Harper 471* (GH, NY). FLORIDA: Duval Co., Jacksonville, *Curtiss 930* (NY), *Wiegand & Manning 2188* (GH, POM); Palm Beach Co., Jupiter, *Curtiss 5545* (NY); Dade Co., Florida City, *O'Neill 7598* (NY, POM); near Cutler, *Small & Carter in 1903* (NY). MISSOURI: Oregon Co., Greer, *Steyermark 27987* (GH, POM). BAHAMAS: Great Bahama, *Brace 3519* (NY). CUBA: La Magdalena, Cayamas, *Baker 4648* (POM); La Puntada la Jaula, *Wright 2554* (GH).

19. LUDWIGIA SIMPSONI Chapman, Fl. S. U.S., ed. 2, 2d Suppl. 685. 1892.

L. cubensis Helwig, Fedde Rep. 25: 53. 1928? Type not seen.

Main leaves spatulate-obovate, 5–15 mm. long, 3–7 mm. wide; petioles 1–3 mm. long; bracteoles 1–2 mm. long; sepals 1.5–2 mm. long; capsule 2–2.5 mm. long, almost as wide, obscurely angular.

Type locality: Manatee, Manatee Co., Fla. Ranging from Wakulla Co., Fla. to Dade Co. and in Cuba and Jamaica. *Representative material:* FLORIDA: Wakulla Co., St. Marks, *Rugel in 1843* (NY); Alachua Co., near Waldo, *Wiegand & Manning 2189* (GH, POM); Orange Co., Sanford, *Nash 2278* (GH, NY); Manatee Co., Manatee, *Simpson*, type coll. (GH, photo POM), *Tracy 7602* (GH, NY); Lee Co., Ft. Myers, *Hitchcock 117* (GH, NY); Palm Beach Co., Jupiter, *Curtiss 5545* (GH, NY, POM); Monroe Co., Pine Key, *Blodgett* (GH, NY); Dade Co., Camp Jackson, *Small & Wilson 1808* (NY). CUBA: Isle of Pines, San Juan, *Britton, Britton & Wilson 15527* (GH, NY). JAMAICA: Black River, *Harris 9935* (NY).

20. LUDWIGIA SPATHULIFOLIA Small, Man. Southeast. Fl. 943, 1506. 1933. Published without Latin diagnosis, but valid according to Rules, because of date.

Main leaves spatulate, denticulate toward apex, 1–1.5 cm. long, 3–6 mm. wide, with poorly defined winged petioles 2–9 mm. long; bracteoles 2–2.5 mm. long; sepals 2 mm. long; capsule 3–4.5 mm. long, almost as wide at apex, somewhat rounded at angles.

Type locality: Everglades, northwest of Perrine, Dade Co., Fla. *Material seen:* FLORIDA: Lee Co., Ft. Myers, *J. Standley 76* in part (GH, NY); Dade Co., Royal Palm Hammock, *Small, Mosier & Small 6644* (GH, NY); near Perrine, *Small & Carter 2990*, type no. (NY); Humbugus Prairie, *Small & Mosier 5619* (NY); Camp Jackson, *Small & Wilson 1848* (NY).

21. LUDWIGIA CURTISSII Chapman, Fl. S. U. S., Suppl. 621. 1883.

Main leaves oblanceolate-spatulate, denticulate at apex, 1–1.5 cm. long, 1–4 mm. wide, with winged petioles 1–5 mm. long; bracteoles about 2 mm. long; sepals deltoid-lanceolate, 2–2.5 mm. long; capsule 2.5–3.5 mm. long, about as wide.

Type locality given as "East Florida (*Curtiss*)," the Curtiss distribution no. 922 on which the labels say "Ludwigia Curtissii, Chapm. n.sp." coming from "Ponds near Cape Malabar, Florida," which I take to be the type locality. *Material seen* all from pinelands of southern FLORIDA: Manatee Co., Bradentown, *Cuthbert 1364* (NY); Indian River Co., Felsmere, *Small 8884* (NY); Cape Malabar, *Curtiss 922*, type no. (GH, NY, photo POM); Lee Co., Myers, *Hitchcock 115* (GH, NY); Chapin, *Hitchcock 116* (GH, NY); Monroe Co., Pine Crest, *Moldenke 856a* (NY); Dade Co., near Miami, *Small 4023* (NY).

22. LUDWIGIA LINIFOLIA Poir. in Lam. Encycl. Suppl. **5**: 513. 1813.

Isnardia linifolia Kuntze, Rev. Gen. **1**: 251. 1891.

Leaves of stolons elliptic-obovate to oblanceolate 5–13 (15) mm. long; main cauline leaves linear, acute, sessile, 1–3.5 cm. long, 1–2.5 mm. wide; flowers rather crowded, sessile; bracteoles 1.5–3 mm. long; sepals lance-linear, 4–6 mm. long; petals narrow-obovate, 4–6 mm. long; capsule sub-cylindric, 8–9 mm. long, 1.5 mm. thick, with somewhat corky wall.

Type locality: "croît dans l'Amérique septentrionale." Found in pine-barrens from North Carolina to Florida and Mississippi. *Represented by:* N. CAROLINA: *Godfrey 6195.*

GEORGIA: *Harper 646* and *1109*. FLORIDA: *Wiegand & Manning 2186, Curtiss 922, 4322, Nash 1240, Fredholm 5378, 5737, Hitchcock 119*, ALABAMA: *Harper 3805*. MISSISSIPPI: *Lloyd & Tracy 225*.

23. LUDWIGIA STRICTA Wright ex Sauvalle, Fl. Cubana 54. 1873.

Isnardia stricta Wright ex Griseb. Cat. Pl. Cub. 107. 1866.

Leaves of stolons elliptic-spatulate, 5–8 mm. long, the principal cauline ones oblance-spatulate, 1–2 cm. long, 2–5 mm. wide; bracteoles scarcely 1 mm. long; sepals deltoid-ovate to -lanceolate, about 2 mm. long; petals 3–5 mm. long; capsule subterete, 5–7 mm. long, 1–2 mm. thick.

Type locality not stated; the Wright specimen at Gray Herb. says Lagunas Vueltalago, so far as I can read it. *Material seen* of the species: CUBA: *Wright 2555*, type no. (GH); Piñar del Río, near Herradura, *Britton, Britton, Earle & Gager 6613* (NY); near Piñar del Río, *Britton, Britton and Gager 7233* (NY).

24. LUDWIGIA LINEARIS Walter, Fl. Car. 89. 1788.

Leaves of stolons obovate to elliptic, about 1 cm. long; main cauline leaves linear to linear-elliptic, 2.5–6 cm. long, 1.5–5 mm. wide, sessile; flowers sessile in uppermost axils, from few to about a dozen per branch; bracteoles 1–3 mm. long; sepals lance-deltoid, glabrous to puberulent, 2.5–4 mm. long; petals 3.5–5 mm. long; capsule elongate obpyramidal, 6–8 mm. long, about 3 mm. thick.

24a. L. LINEARIS Walt. var. **typica** Munz, var. nov.

L. linearis Walt. Fl. Car. 89. 1788. *Isnardia linearis* DC. Prodr. **3**: 60. 1828. *Ludwigia angustifolia* Michx. Fl. Bor. Am. **1**: 88. 1803.

Stems and leaves glabrous or somewhat strigulose on veins, etc.; hypanthium and sepals minutely granular-strigulose.

Type locality: Carolina. Found in moist places, mostly in pine-barrens from New Jersey to Florida, Tennessee, and eastern Texas. Western material gradually becomes more strigulose and passes into

24b. L. LINEARIS var. PUBERULA Engelm. & Gray, Pl. Lindh. 9 (Boston Journ. Nat. Hist. **5**). 1845.

Whole plant rather densely and closely puberulent.

Type locality: Houston, Texas. Ranging from Mississippi and so. Arkansas to eastern Texas. *Represented by:* MISSISSIPPI: Smith Co., Taylorville, *Tracy 8715* (GH, NY). ARKANSAS: Ashley Co., Mist, *Demaree 18040* (NY, POM). TEXAS: Newton Co., near Deweyville, *Cory 10904* (GH); Hardin Co., Silsbee, *Cory 19965* (GH); Waller Co., Hempstead, *E. Hall 221* in part (NY, POM); Harris Co., Houston, *Lindheimer 58*, type no. (GH); Brazoria Co., Columbia, *Bush 1542* (GH, NY).

25. LUDWIGIA GLANDULOSA Walt. Fl. Car. 88. 1788.

Leaves of stolons elliptic-ovate to -obovate, the blades 1–2 cm. long, petioles 5–10 mm. long; main cauline leaves mostly lanceolate, the blades 3–10 cm. long, 6–20 mm. wide, on petioles 3–10 mm. long; bracteoles scarcely 1 mm. long; sepals deltoid to almost lanceolate, 1–2 mm. long; petals none;

capsules sessile, subcylindric, sometimes 4-grooved, 2–8 mm. long, 1.5–2 mm. thick.

25a. L. GLANDULOSA Walt. var. **typica** Munz, var. nov.

L. glandulosa Walt. Fl. Car. 88. 1788. *L. cylindrica* Elliott, Sketch Bot. S. Car. & Ga. 1: 213. 1817. *Isnardia cylindrica* DC. Prodr. 3: 60. 1828. *Jussiaea brachycarpa* Lam. Encycl. 3: 331. 1789. *Ludwigia heterophylla* Poir. in Lam. Encycl. Suppl. 3: 512. 1813.

Hypanthium and sepals mostly quite glabrous; sepals 1.5–2 mm. long; capsule 6–8 mm. long.

Type locality: Carolina. Ranging from Virginia to northern Florida and the Gulf states, and from southern Illinois and Indiana to eastern Texas.

25b. L. GLANDULOSA Walt. var. **Torreyi** Munz, nom. nov.

L. cylindrida Ell. β *brachycarpa* Torrey & Gray, Fl. N. Am. 1: 524. 1840; not *Jussiaea brachycarpa* Lam. Encycl. 3: 331. 1789.

Hypanthium and sepals minutely strigulose; sepals 1–1.5 mm. long; capsules 2–4 mm. long.

So far as I can determine, Torrey & Gray had in mind Lamarck's name *brachycarpa* for their variety, but I have seen a photograph of his type and it is long-fruited. They cited a Chapman collection from Florida and one by E. Hall, no. 219, from Hempstead, Texas. Since this has a definite locality, I propose it be taken as the type collection.

This variety is represented by: FLORIDA: without definite locality, *Chapman* (NY). LOUISIANA: Cameron, *Tracy 8496* (GH, NY). TEXAS: Dallas, *Reverchon* (GH, NY); Robertson Co., College Station, *Reverchon 2000* (NY); Brazos Co., Wellborn, *Reeves 938* (POM); Brazoria Co., *Bush 1399* (NY).

UNCERTAIN AND EXCLUDED SPECIES OF LUDWIGIA

L. angustifolia (Lam.) Gomez, An. Hist. Nat. Madrid 23: 66. 1894 is *Jussiaea suffruticosa* var. *ligustrifolia* (HBK.) Griseb.

L. Bertonii Lévl. in Bertoni, Descr. Fis. Econ. Parag. 3: 1910 may be a *Jussiaea*.

L. brachycarpa DC. Prodr. 3: 55. 1828, in obs., is probably *Jussiaea brachycarpa* Lam., hence *L. glandulosa* Walt. var. *typica*.

L. Clavellina var. *grandiflora* Gomez, l. c. is *Jussiaea uruguayensis* Camb.

L. Clavellina var. *peploides* Gomez, l. c. is *Jussiaea repens* var. *peploides* (HBK.) Griseb.

L. decurrens Walt. Fl. Car. 89. 1788 is *Jussiaea decurrens* (Walt.) DC.

L. diffusa Greene var. *californica* Greene, Fl. Francisc. 227. 1891 is *Jussiaea repens* var. *peploides* (HBK.) Griseb.

L. foliosa Gomez, l. c. is *J. leptocarpa* var. *angustissima* Helwig.

L. hastata Spreng. Syst. 1: 446. 1825 (*Isnardia hastata* R. & P. Fl. Peruv. 1: 66, *pl. 85, f. 6.* 1798) is *Ammania latifolia* L. acc. Kew Index.

L. hirta Gomez, l. c. is *Jussiaea peruviana* L.

L. hondurensis Standl. Field Mus. Pub. Bot. 8: 146. 1930 is *Jussiaea nervosa* Poir.

L. inclinata Gomez, l. c. is *Jussiaea inclinata* L. f.

L. juncea Raf. Autik. Bot. 38. 1815–1840; questionably referred to *L. virgata* Michx. in Kew Index. The small flowers suggest *L. alternifolia* L., but the description is inadequate.

L. jussiaeoides Michx. Fl. Bor. Am. 1: 89. 1820 is *Jussiaea decurrens* DC.

L. lutea Bose ex DC. Prodr. 3: 60. 1828, pro synon. under *L. virgata*.

L. oocarpa Gomez, l. c. is *Oocarpon torulosum* (Arnott) Urban.

L. palustris L. var. *Liebmanni* Lévl. Bull. Géogr. Bot. 22: 24. 1912; referred to synonymy under *L. palustris* var. *americana* by Fernald & Griscom, Rhodora 37: 176. 1935. The description sounds like their var. *nana*, over which name it would have priority, but it may even belong under *L. natans*.

L. peduncularis Gomez, l. c. is *Jussiaea peduncularis* Wright.

L. pruinosa Raf. Autik. Bot. 38. 1815–1840. "From Alleghany Mts. and Kentucky," a fact limiting the possibilities. Cannot be *L. alternifolia* L., to which referred by Index Kewensis, because of long petals and sessile leaves. I cannot place it definitely.

Isnardia ramosior L. ex Jackson, Index Linn. Herb. 91. 1912; nomen?

L. ramosissima Roth, Catalect. fasc. 3: 24. 1806; from description is in sect. *Dantia*, near *L. palustris* or *L. natans*.

L. ramulosa Gomez, l. c. is *Jussiaea repens* var. *peploides* (HBK.) Griseb.

L. rudis Walt. Fl. Car. 89. 1788; according to Torrey & Gray, Fl. N. Am. 1: 526. 1840 there are no specimens in the Walter Herb.; I do not place it.

L. Sagraeana Gomez, l. c. is *Jussiaea suffruticosa* var. *ligustrifolia* (HBK.) Griseb.

L. scabriuscula Kell. Proc. Calif. Acad. 7: 78. 1876; is *Ammania latifolia* L. according to Kew Index.

Isnardia subhastata R. & P. Fl. Peruv. 1: 66. 1798; is *Ammania latifolia* according to Kew Index.

L. Swartziana Baill. ex Laness. Pl. Util. Colon. Franc. 457. 1866 from Martinique; unknown to me.

L. tepicana M. E. Jones, Contr. W. Bot. 15: 131. 1929; is *Heimia salicifolia;* cf. Standley, Field Mus. Pub. Bot. 8: 28. 1930.

L. tuberosa Raf. Ann. Nat. 15. 1820; *L. virgata* ? according to Kew Index, but from wrong region. I cannot place it.

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DROSERA IN EASTERN NORTH AMERICA

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Confusion in the current manuals among *Drosera longifolia*, *Drosera anglica*, and *Drosera intermedia* has led to the present investigation of the eastern species of sundew. The puzzle was found to result from a nomenclatural tangle between two clear-cut species.

Linnaeus described *Drosera longifolia* in 1753 in his *Species Plantarum*. Hudson described *Drosera anglica* in 1778 in the *Flora Anglica*, and in 1800 Hayne proposed *Drosera intermedia* in Schrader's *Journal für die Botanik*.

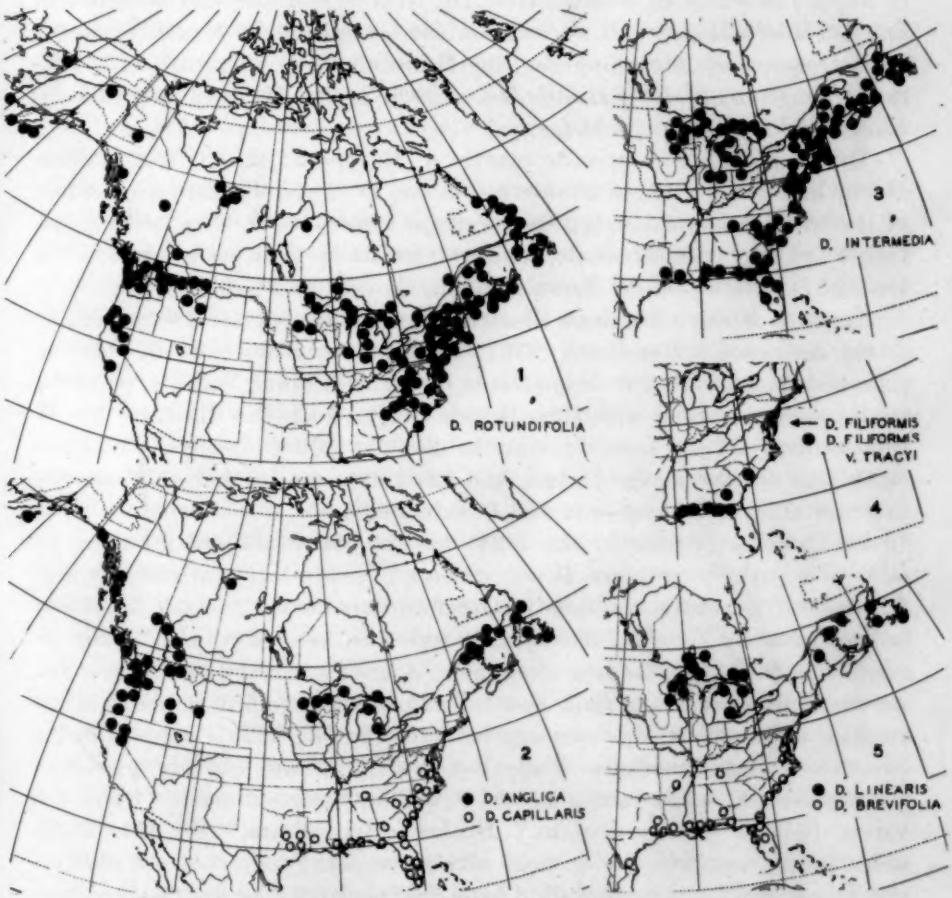
Herbarium specimens labelled *D. longifolia*, *D. anglica*, and *D. intermedia* were examined. They fall into two groups on the basis of their stipules and seeds. Group 1 is characterized by adnate stipules, and black, fusiform, striate-areolate seeds. Group 2 has free stipules and brown, oblong, papillose seeds. The leaves in group 1 tend to be elongate-spatulate, whereas those in group 2 tend to be obovate. However, some plants in each could, on the basis of their leaves, be placed in the other group, so that leaf characters alone cannot be used as a basis for specific distinctions.

The distribution of groups 1 and 2 was mapped and the ranges were found to be characteristic and distinct. Group 1 occurs in the Rocky Mountains, around the Great Lakes, and in Eastern Quebec and Newfoundland (fig. 2). Group 2 occurs along the coast of eastern North America from Newfoundland to Louisiana and around the Great Lakes (fig. 3). The ranges overlap in only two areas—the Great Lakes region and in eastern Canada.

The next problem was determining the correct names applicable to the two species. I am proposing, for the reasons discussed in the following pages, the adoption of *D. anglica* Huds. for the plants in group 1 and of *D. intermedia* Hayne for those in group 2. Linnaeus' *D. longifolia* is the oldest name and it should be used if we could determine whether it was originally applied to the plant here called *D. anglica*, or to *D. intermedia*, or to both. Neither the original description nor pre-Linnaean references mention the only satisfactory characters by which they may be separated—the stipules and the seeds. Leaf shape, which *is* described, cannot be used to determine what plant Linnaeus had. Furthermore, no report of an examination of Linnaeus' type is known to the author.

If we trace the interpretation of the species of *Drosera* through the literature, we find continuous nomenclatural confusion. In Hudson's treatment of *Drosera* in 1778 (Fl. Angl., 135) he proposed *D. anglica* as a new species and recognized also *D. rotundifolia* and *D. longifolia*. The distinguishing characters he gives are ". . . floribus . . . hexagynis" and ". . .

capsulis trivalvis'' for *D. longifolia,* and ''. . . floribus octogynis'' and ''. . . capsulis quadrivalvis'' for *D. anglica.* By 1800, however, it had been observed by Hayne that this division of the capsule into 3 or 4 (and sometimes 5) parts is not constant within a species but occurs occasionally in all the species. Early botanists, nevertheless, often gave capsule characters as the only differences between these closely related species.



FIGS. 1–5. Distribution in North America of the species of *Drosera.*

Smith in his *Flora Britannica* (**1**: 347. 1800) uses *D. longifolia* and *D. anglica* in the same sense as Hudson. He adds a distinction in the leaf shape: *D. longifolia* is described as ''foliis obovatis'' and *D. anglica* as ''foliis oblongis obtusis.''

Hayne in treating *Drosera* in Schrader's *Journal für die Botanik* (**1800**(1): 37–39. 1801) includes the species *D. rotundifolia, D. longifolia,*

and his new species *D. intermedia*. In the list of distinguishing features for *D. intermedia* is found: "4) *Capsula* tri—s. quadrivalvi, nec quadri—s. quinquevalvi. 5) *Seminibus* obovatis, verrucosis, *arillo* destitutis." *D. longifolia* is described in part as follows: "*Capsula* . . . quadri—s. quinquevalvis . . . Semina . . . *arillo* scobiformi, membranaceo, reticulatim venoso tecta." Schrader has added the following in a footnote: "Nach einem Exemplare der *D. anglica* zu schliesen, welches Herr Dr. Nohden von England mitgebracht hat, ist Herrn Hayne's *D. intermedia* die eigentliche *D. longifolia* Linn., seine *D. longifolia* aber hingegen, die Hudson'sche *D. anglica*." It is true that Hayne's *longifolia* is Hudson's *anglica*. Whether Hayne's *intermedia* is Linnaeus' *longifolia* is problematical.

Dreves & Hayne (Choix de plantes d' Europe **1**: 42, 43. 1802) follow Hayne and use the names *D. intermedia* and *D. longifolia* with no mention of Hudson's *D. anglica* among the species or synonyms. *D. longifolia* is illustrated (*pl. 75*) with attenuate, fusiform, striate-areolate seeds whereas the seeds of *D. intermedia* are shown as blunt, obovate, and papillose.

Seeds of *Drosera* had been illustrated only once prior to 1802. Schkuhr in the *Botanisches Handbuch* (1791) illustrates and describes *D. rotundifolia* and *D. longifolia*. *D. longifolia* is shown with blunt, obovate, papillose seeds—seeds identical with those which Dreves & Hayne illustrate for *D. intermedia*. Schkuhr, however, since he does not split *D. longifolia* L., obviously had *D. intermedia* Hayne, and his treatment further confuses the interpretation of *D. longifolia* and *D. intermedia*.

De Candolle (Prodr. **1**: 318. 1824) was the first to discard the name *D. longifolia* entirely and use *D. intermedia* ("seminibus exarillatis") and *D. anglica* ("seminibus arillatis"). Other authors use the name *D. longifolia* indiscriminately for first one species and then the other with either *D. anglica* or *D. intermedia* as a companion. A brief summary of the most important publications will show how the names were shuffled. Schultes in his revision of Linnaeus' *Systema vegetabilium* (**6**: 761. 1820) includes in his description of *D. longifolia* "Caps. 3–4—valvis. Semina obovata, glandulis elevatis obsessa, arillis destituta." Of *D. anglica* he says in part: "Caps. 4–5 valvis. Semina arillo-reticulato." Hooker (Brit. Flora, 148, 149. 1830) describes *D. longifolia* ". . . seeds with a compact rough coat not chaffy" and *D. anglica* ". . . seeds with a loose chaffy coat." The contrasting characters are given as follows: "Here [*D. anglica*] the seed . . . has a very loose, reticulated, even coat. In *D. longifolia* the coat firmly adheres to the rest of the seed, and is rough or papillose." Koch (Synopsis, 90. 1837) treats *D. anglica* as a synonym of *D. longifolia* L. and includes also *D. intermedia*. Torrey and Gray (Fl. N. Am. **1**: 146. 1838) use *D. longifolia* for the plant with "seeds oblong, slightly punctate, the testa not arilliform" and *D. anglica* for the plant which has "seeds with an arilliform testa." In *Flora*

Rossica (**1**: 261. 1842) Ledebour includes *D. longifolia* and *D. intermedia* with *D. anglica* placed as a synonym of *D. longifolia*. He does not mention the seeds in his diagnostic characters. Grenier & Godron in *Flore de France* (192. 1847) say of *D. longifolia:* "Graines oblongues-ovoïdes, *un peu rugueuses;* épisperme lâche, prolongé aux deux extrémités" and of *D. intermedia:* "Graines ovales-oblongues, *fortement* tuberculeuse, à épisperme ou teste *exactement appliqué.*"

Planchon, however (Ann. Sci. Nat. III. **9**: 198–200. 1848), follows de Candolle, discarding *D. longifolia* L. entirely and using *D. intermedia* and *D. anglica*. Watson (Index, part 1, 353, 354. 1878), Macoun (Canadian Plants **1**: 165, 166. 1883), and Parlatore (Fl. Ital. **9**: 212–216. 1890) do likewise.

It is apparent, then, that the literature in the century and a half following Linnaeus can be of little help in indicating which plant Linnaeus described as *D. longifolia*. It is likewise apparent that since 1800 two distinct species have been recognized. The epithet *longifolia* has been used for both these species. For the sake of argument let us call the plant with striate-areolate seeds *D. anglica* and the one with papillose seeds *D. intermedia*. Then wherever *D. longifolia* and *D. anglica* are recognized let us substitute *D. intermedia* for *D. longifolia;* where *D. longifolia* and *D. intermedia* are recognized let us substitute for *D. longifolia, D. anglica*. We then find the nomenclatural confusion eliminated and the concept of *D. anglica* and *D. intermedia* consistent and clear.

Current manuals remain confused in their nomenclature. *D. anglica* with adnate stipules and "loosely faveolate" [sic.] seeds and *D. longifolia* with stipules nearly free and papillose seeds are included in Gray's Manual (ed. 7, 440. 1908). Britton and Brown (Ill. Fl. **2**: 203, 204. 1936) and Rydberg (Fl. Prairies and Plains, 386. 1932) use the name *D. intermedia* for the plant with papillose seeds and the name *D. longifolia* for the plant with striate-areolate seeds. Only one of these two species occurs in southern United States and *D. intermedia* has been consistently used in the manuals covering this area. The other species occurs in the west and it has been called *D. longifolia* in manuals for that area.

The preceding synopsis does not cite every publication in which *D. intermedia, D. longifolia,* and *D. anglica* have been used. It is sufficient, however, to indicate the continuous confusion that has existed ever since the three names appeared in the literature. Since it is impossible to determine to which species the name *D. longifolia* should be applied, it is the author's opinion that the name should be abandoned as a source of confusion until the type can be examined. An examination of the type is impossible at the present time. Article 62 of the *International Rules of Botanical Nomenclature* (ed. 3. 1935) states: "A name of a taxonomic group must be rejected if, owing to

its use with different meanings, it becomes a permanent source of confusion or error." Therefore, *D. longifolia* should be rejected and *D. anglica* and *D. intermedia* should be adopted. If, at a subsequent date, an examination of the Linnaean type of *D. longifolia* is possible, it would be necessary to substitute the name *D. longifolia* for one of the other two names. Until such time, however, the author proposes the following treatment which adopts both *D. anglica* and *D. intermedia* and rejects *D. longifolia* as a *nomen ambiguum*. This was done by several authors mentioned above and by Diels in Engler's *Das Pflanzenreich*. The author knows of only one recent treatment of North American plants which has adopted this procedure (Trans. Wis. Ac. **27**: 235. 1932).

The other eastern species of *Drosera*, with the possible exception of *D. filiformis* var. *Tracyi*, present no problems. In 1914 Macfarlane proposed *D. Tracyi* as a new species. Previously, however, in 1906, Diels in *Das Pflanzenreich* published *D. filiformis* var. *Tracyi* "(Macfarlane msc. sub. titulo speciei)." Because the plant which grows along the coast from South Carolina to Mississippi differs from the one which grows on the coast from Massachusetts to Delaware only in its size and the color of pubescence, the author is following Diels and maintaining the southern variant as *D. filiformis* var. *Tracyi*. In all other characters of leaves, stipules, flowers, and seeds it is identical with the more northern *D. filiformis*.

Seven species of *Drosera* occur in eastern North America. Heretofore, no emphasis has been placed on characters presented by the seeds of sundews. In fact, they have been too briefly and inaccurately described and never adequately illustrated. This is unfortunate, for the seeds of the seven species are beautifully distinct and offer a great aid in identification. Using only leaf shape, it is not always possible to distinguish *D. intermedia* from *D. anglica;* and the leaves of certain forms of *D. capillaris* and *D. brevifolia* can be mistaken for *D. rotundifolia*. However, by means of stipules and seeds the species of *Drosera* in eastern North America are easily separated. For this reason the seeds are carefully described and illustrated here.

DROSERA L. Gen. Pl. 89. 1737; Sp. Pl. 281. 1753.

Rorella Hall, *in* Rupp. Fl. Jen. 114. 1745.
Esera Neck. Elem. Bot. 2: 160. 1790.
Dismophyla Raf. Fl. Tellur. 3: 36. 1836.
Adenopa Raf. Fl. Tellur. 3: 37. 1836.
Filicirna Raf. Fl. Tellur. 3: 37. 1836.
Sondera Lehm. Pugill. 8: 44. 1844.

Annual, biennial, or perennial insectivorous herbs of bogs and marshes. Leaves alternate, usually basal, tufted, covered with long glandular hairs which copiously exude a clear, viscid secretion. Blades filiform to peltate, circinate in vernation. Stipules scarious, variously fringed or divided, adnate or free (lacking in one of our species). Inflorescence a cincinnus [not

a raceme], nodding at the undeveloped apex. Flowers regular, hypogynous, generally pentamerous. Sepals 4–8 (usually 5), withering-persistent, distinct or united at the base. Petals 4–8 (usually 5), white, pink, or purple, broadened at the tip, distinct or slightly united at the base. Stamens 4–8, as many as the petals, with subulate or filiform filaments and extrorse, versatile anthers. Ovary superior, sessile, 1-celled, many-ovuled with 3–5 parietal placentae. Ovules subglobose or ovoid in 2–5 rows on each placenta. Styles 2–5, (usually 3), bipartite to the base. Capsule 2–5 (usually 3) valved. Seeds minute, anatropous, numerous, stipitate; the testa loose and variously reticulated and ornamented.

Leaf-blades filiform, not distinct from the petiole ..... 1. *D. filiformis.*
Leaf-blades expanded, distinct from petiole.
  Leaf-blades suborbicular, broader than long; seeds sigmoid-fusiform, finely longitudinally striate ..... 2. *D. rotundifolia.*
  Leaf-blades linear, spatulate, or cuneate; seeds variously ornamented.
    Stipules adnate.
      Leaf-blades linear; seeds rhomboidal, crateriform, 0.5–0.8 mm. long ..... 3. *D. linearis.*
      Leaf-blades elongate-spatulate; seeds fusiform, areolate-striate, 1–1.5 mm. long ..... 4. *D. anglica.*
    Stipules free or lacking.
      Stipules conspicuous, free, scape glabrous.
        Flowers white, 7–8 mm. in diameter, petals 4–5 mm. long; seeds irregularly and densely covered with long papillae, 0.7–1.0 mm. long ..... 5. *D. intermedia.*
        Flowers pink, 10 mm. in diameter, petals 6–7 mm. long; seeds papillose-corrugated with 14–16 ridges, 0.4–0.5 mm. long ..... *D. capillaris.*
      Stipules absent, scape glandular-pubescent, seeds crateriform, 0.3–0.4 mm. long ..... 7. *D. brevifolia.*

1. DROSERA FILIFORMIS Raf. Med. Rep. II. **5**: 360. 1808; in Desv. Jour. de Bot. **1** (1808): 227. 1809.

Drosera tenuifolia Willd. Enum. 340. 1809.

Stem 1–2 cm. long. Leaves erect, basal, filiform, without distinction between blade and petiole, 8–35 cm. long, covered with long, purple or green glandular hairs. Stipules adnate, fimbriate on margins, forming matted brown wool at the base of the leaves. Scape glabrous, 6–45 cm. long, bearing 4–26 flowers. Calyx and upper part of pedicel glandular-pubescent. Flowers 1–2 cm. in diameter. Sepals oblong to elliptic, glandular-pilose, 4–7 mm. long, 2–2.5 mm. wide, united at base. Petals purple (rarely white), broadly ovate, 7–15 mm. long, 5–15 mm. wide, erose at apex. Styles 3, bi-partite to the base. Capsule obovoid, 5–6 mm. long. Seeds black, 0.5–0.8 mm. long, elliptic, abruptly caudate at both ends, coarsely crateriform, the pits in 16–20 lines. Fig. 7.

DROSERA FILIFORMIS var. **typica** Wynne, var. nov.

D. filiformis Raf. Med. Rep. II. 5: 360, as to type. 1808.

Leaves 8–25 cm. long, covered with long purple glandular hairs. Scape 6–22 cm. long, bearing 4–16 flowers. Flowers about 1 cm. in diameter; petals 7–15 mm. long, 5–8 mm. wide.

Along the coast from Massachusetts to Delaware. Fig. 4.

DROSERA FILIFORMIS var. TRACYI (Macfarlane) Diels in Engler, Pflanzenreich **26** (IV. 112): 92. 1906.

Drosera tracyi Macfarlane in L. H. Bailey, Stand. Cyc. Hort. 2: 1077. 1914.

Differs from var. *typica* only in its pale green pubescence, larger size, and more robust habit. Leaves 25–35 cm. long, covered with long green glandular hairs. Scape 25–45 cm. tall, bearing 14–26 flowers. Flowers 1.5–2 cm. in diameter; petals 12–15 mm. long, 15 mm. wide.

Abundant in the coastal area of the Gulf states from mid-Florida to Louisiana; also in Georgia and South Carolina. Fig. 4.

2. DROSERA ROTUNDIFOLIA L. Sp. Pl. 281. 1753.

D. septentrionalis Stokes, Bot. Mat. Med. 2: 189. 1812.
D. rotundifolia var. *comosa* Fern. Rhodora 7: 9. 1905.

Stem 1–2 cm. long bearing a rosette of leaves. Petiole 1.5–5 cm. long, flat, glandular-pilose. Leaf-blade suborbicular, 0.4–1 cm. long, broader than long and much shorter than the petiole. Stipules 4–6 mm. long, adnate, fimbriate along the upper half. Scape glabrous, 7–35 cm. long, bearing 3–15 (1–25) flowers. Flowers about 4–7 mm. in diameter. Sepals oblong, 4–5 mm. long, 1.5–2 mm. wide, obtuse, united at base. Petals white to pink, spatulate, longer than the sepals, 5–6 mm. long, 3 mm. wide. Styles 3, bipartite. Capsule 5 mm. long. Seeds light brown, 1–1.5 mm. long, sigmoid-fusiform, finely and regularly longitudinally striate, shiny with a metallic luster. Fig. 6.

Common in bogs and swamps in northern North America south to California, Montana, Illinois, Wisconsin, Ohio, South Carolina, and Georgia. Fig. 1.

3. DROSERA LINEARIS Goldie, Edinb. Phil. Jour. **6**: 325. 1822.

Stem 1–2 cm. long with a rosette of erect leaves. Petiole 3–7 cm. long, glabrous, flattened. Leaves linear, 2–5 cm. long, about 2 mm. wide. Stipules 5 mm. long, adnate, fimbriate along the margins. Scape glabrous, 6–13 cm. long, bearing 1–4 flowers. Flowers about 6–8 mm. in diameter. Sepals oblong-elliptic, minutely glandular-denticulate, 4–5 mm. long, 2 mm. wide, united at base. Petals white, obovate, 6 mm. long, 3–4 mm. wide. Styles 3, bipartite to the base. Capsule 4–5 mm. long. Seeds black, 0.5–0.8 mm. long, rhomboidal, oblong-obovate, densely and irregularly crateriform. Fig. 8.

In northeastern North America extending south to Maine, Michigan, and Wisconsin. Fig. 5.

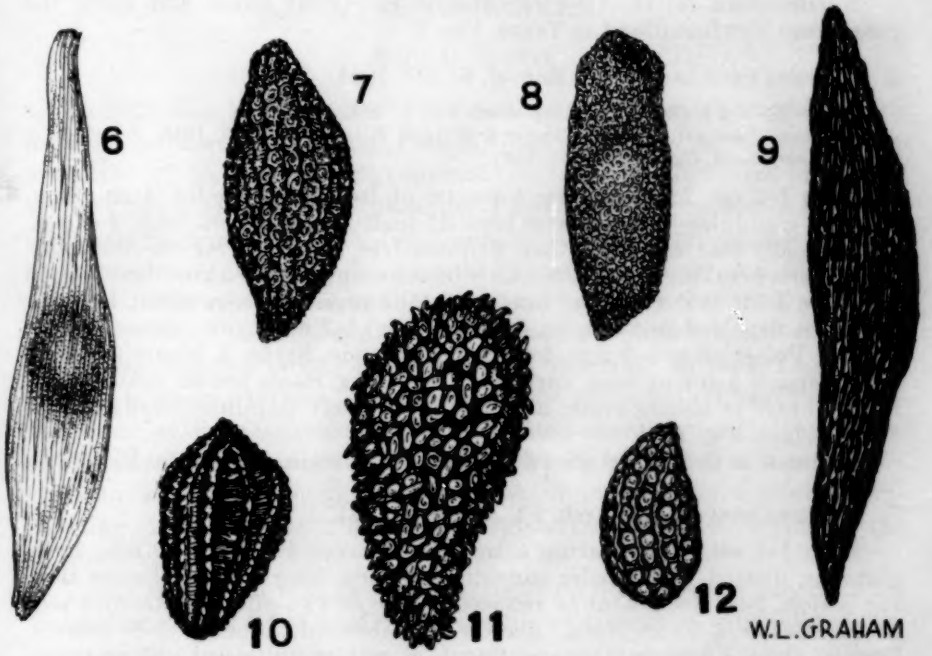
4. DROSERA ANGLICA Huds. Fl. Angl. ed. 2, 135. 1778.

D. anglica, Gray, Man. ed. 7, 441, 1908.
D. longifolia, Britton & Brown, Ill. Fl. 2: 204. 1936; Rydberg, Fl. Prairies & Plains, 386. 1932.

Stem 1–2 cm. long bearing a rosette of leaves. Petioles 3–7 cm. long, glabrous or sparsely glandular hairy. Leaves obovate to elongate-spatulate, 3–4 mm. wide, 15–35 mm. long, with long glandular hairs on the upper surface. Stipules 5 mm. long, adnate along the entire length, fimbriate along the upper half. Scape glabrous, 6–25 cm. long, bearing 1–9 flowers. Flowers 6–7 mm. in diameter. Sepals oblong, minutely glandular-denticulate, 5–6 mm.

long, united at the base. Petals white, spatulate, 6 mm. long. Styles 3, bipartite to the base. Capsule minutely tuberculose, 4–6 mm. long. Seeds 1–1.5 mm. long, black, sigmoid-fusiform, longitudinally striate-areolate. Fig. 9.

In western North America, around the Great Lakes, and in eastern Canada. Fig. 2.



Seeds of *Drosera*. FIG. 6. *D. rotundifolia*. FIG. 7. *D. filiformis*. FIG. 8. *D. linearis*. FIG. 9. *D. anglica*. FIG. 10. *D. capillaris*. FIG. 11. *D. intermedia*. FIG. 12. *D. brevifolia*. All × 80.

5. DROSERA INTERMEDIA Hayne in Schrad. Jour. Bot. **1800** (1): 37. 1801.

D. longifolia Michx. Fl. Bor. Am. **1**: 186. 1803.
D. americana Willd. Enum. 340. 1809.
D. foliosa Elliot, Sketch **1**: 376. 1817.
D. intermedia β *corymbosa* DC. Prodr. **1**: 318. 1824.
D. intermedia γ *americana* DC. Prodr. **1**: 318. 1824.
D. longifolia Gray, Man. ed. 7, 441. 1908.
D. intermedia Britton & Brown, Ill. Fl. **2**: 203. 1936; Rydberg, Fl. Prairies and Plains, 386. 1932.
D. intermedia f. *corymbosa* Fern. Rhodora **40**: 333. 1938.

Stem 1–8 cm. long, bearing leaves in a rosette and/or at intervals for several centimeters along the stem. Petioles 2–5 cm. long, glabrous. Leaves oblong spatulate to obovate, 4–5 mm. wide, 8–20 mm. long, bearing long glandular hairs on the upper surface. Stipules adnate at the base for the first millimeter, then breaking into several setaceous segments 2–5 mm. long. Scape erect, glabrous, 9–20 cm. long, bearing 9–20 flowers. Flowers 7–8 mm.

in diameter. Sepals oblong, 3–4 mm. long, 1–1.5 mm. wide, united at base. Petals white, 4–5 mm. long, 3–5 mm. wide. Styles 3 (rarely 4), bipartite. Capsule 4–5 mm. long. Seeds 0.75–0.95 mm. long, reddish brown, oblong, blunt at the ends, densely and irregularly covered with long papillae. Fig. 11.

Northeastern North America; around the Great Lakes and along the coast from Newfoundland to Texas. Fig. 3.

6. DROSERA CAPILLARIS Poir. Encycl. **6**: 299. 1804.

D. brevifolia β *major* Hook. Hook. Jour. Bot. 1: 194. 1834.
D. rotundifolia var. *capillaris* Eaton & Wright, N. Am. Bot. 230. 1840.
D. minor Wood, Class-Book, 251. 1861.

Stem 1–2 cm. long, bearing a rosette of leaves. Petiole 0.6–4 cm. long, sparsely glandular-pilose. Leaves broadly spatulate, 0.5–1 cm. long, 3–5 mm. wide, usually shorter than petiole. Stipules free, or adnate for the first millimeter, then breaking into numerous setaceous segments 3–5 mm. long. Scape glabrous, 4–20 (35) cm. long, bearing 2–20 flowers. Flowers about 1 cm. in diameter. Sepals oblong-elliptic, 3–4 mm. long, 1–2 mm. wide, obtuse, united at base. Petals pink, 6–7 mm. long, 2–3 mm. wide. Styles 3, bipartite to the base. Capsule 4–5 mm. long, surpassing the calyx. Seeds brown, 0.4–0.5 mm. long, elliptic to oblong-ovate, asymmetric, coarsely papillose-corrugated in 14–16 ridges. Fig. 10.

Common in the coastal area from southern Virginia to Texas. Fig. 2.

7. DROSERA BREVIFOLIA Pursh, Fl. Am. Sept. **1**: 211. 1814.

Stem 1–2 cm. long, bearing a rosette of leaves. Petiole 5–10 mm. long, glabrous, dilated. Leaf-blades cuneate, 4–10 mm. long, usually longer than the petiole. Stipules absent or reduced to one or two minute setaceous segments. Scape 4–9 cm. long, glandular pubescent, bearing 1–8 flowers. Flowers about 1.5 cm. in diameter. Sepals glandular-pubescent, oblong-ovate, 2.5–3.5 mm. long, 1.5–2.5 mm. wide. Petals rose to white, obovate, 4–5 mm. long, 2–3 mm. wide. Styles 3, bipartite to the base. Capsule 3 mm. long. Seeds black, 0.3–0.4 mm. long, obovate, oblong, caudate at base, crateriform, the pits in 10–12 rows. Fig. 12.

In the coastal area, where it is common, from southern Virginia to Texas, Florida, and Missouri. Fig. 5.

EXCLUDED NAME

Drosera longifolia L. Sp. Pl. 281. 1753. *Nomen ambiguum.*

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A DISCUSSION OF THE OCHNACEOUS GENUS FLEURYDORA A. CHEV. AND THE ALLIED GENERA OF THE LUXEMBURGIEAE

JOHN D. DWYER

In 1933 Auguste Chevalier (1) described the genus *Fleurydora* from material collected near Kinda, French Guinea. A study of his description and plate (cf. his figure 1, 1–9) convinced me that Chevalier erred in placing the new genus in the tribe Euthemidae Planchon; this previously consisted of the single genus *Euthemis* Jacq. with six species described from Borneo and Sumatra. Hutchinson (2) recently brought this error to light and reclassified *Fleurydora*, relating it to two American genera of the Ochnaceae, *Blastemanthus* Planchon and *Godoya* R. and P. Unfortunately he resurrected van Tieghem's tribe Blastemantheae, described in 1904, and placed the trio of genera therein. Apparently on the grounds that van Tieghem's treatment of the Ochnaceae is a "celebrated classification," Hutchinson elected to rely on his work to a marked extent. He proceeded in turn to criticize Chevalier's classification without himself manifesting a clear understanding of the complex tribe Luxemburgieae from which he separated the Blastemantheae.

I have spent more than two years in studying the American genera of the Luxemburgieae and feel qualified to discuss relationships within this tribe. Hutchinson's initial error lies in accepting van Tieghem's work without critical analysis. He admits that van Tieghem based his classification "mainly on anatomical characters." Several workers[1] attest to the unsoundness of van Tieghem's study of the Ochnaceae (3), indicating that his criteria of classification are unorthodox, viz., his splitting of the genus *Ouratea* into thirty-four genera and his many new species described without adequate morphological descriptions and accompanying keys.

Fleurydora A. Chev. is obviously not related to the genus *Euthemis* Jacq., since as Hutchinson himself points out, "the tribe Euthemidae is characterized especially by the possession of only *two ovules* in each loculus of the ovary, and in having a baccate fruit composed of five pyrenes." He then reclassifies *Fleurydora*, placing it in the Blastemantheae and indicating the affinity of this tribe with the Luxemburgieae on the basis of its numerous ovules and capsular fruit. Preceding the formal description of his revised

[1] Beauverd, G (Le genre *Luxemburgia*. Bull. Soc. Bot. Genève II. 7: 232. 1916.) states: "... au sens de van Tieghem ... la notion du tribu ... s'applique exactement à nôtre conception du genre. ..." Riley, A. M. (Mexican and Central American Species of *Ouratea*. Kew Bull. **1924**: 102. 1924) points out at some length the weaknesses of van Tieghem's work.

tribe Blastemantheae, Hutchinson asserts that the "character of the very unequal-sized and spirally arranged sepals is shared only by these three genera of the Ochnaceae," *Blastemanthus, Godoya,* and *Fleurydora,* the three genera of his emended tribe. This statement does not agree with the facts, since *Rhytidanthera* van Tieghem, *Krukoviella* A. C. Smith, and *Poecilandra* Tulasne, three American genera of the Luxemburgieae, have unequal sepals similarly arranged. In fact the sepals of *Rhytidanthera*, the only pinnately-leafed genus of the Ochnaceae, are the prototypes of those of *Godoya* in every detail. This character, as well as less obvious characters, demonstrate the close relationship existing between *Godoya* and *Rhytidanthera.* Both of these are closely allied with the genus *Cespedezia* Goudot principally on the basis of the following characters: the fimbriate appendages (glands?) located at the proximal and inner surface of the bracts and sepals, the coriaceous and estylate and pentacarpellate pistil with intrusive T-shaped parietal placentae and with sessile radiating stigmas, and lastly the distinctly alate seeds. *Krukoviella* agrees with the above genera in all these characters except that the sepals lack appendages. Its close relationship with *Godoya* is manifested in the shape, texture, and venation of the leaf-blades, in the texture and shape of the sepals (here often subequal in length), and in the dehiscence of the anthers by a single instead of two terminal pores. The genus *Blastemanthus,* in turn, gives evidence of its relationship with *Godoya, Rhytidanthera, Cespedezia,* and *Krukoviella* in the texture and shape of the sepals, anthers, and pistil, the eccentric position of the pistil at anthesis, and the intrusive T-shaped parietal placentae bearing numerous imbricate ovules. The presence of subulate staminodia links *Blastemanthus* to the remaining American genera of the tribe. While several species of *Poecilandra* have some of their staminodia the prototypes of *Blastemanthus,* the relationship existing between these genera is evident, especially in their vegetative characters. *Blastemanthus* is more closely related to a recently described ochnaceous genus, *Tyleria* Gleason, since it possesses alate seeds and terminally poricidal and unequal-celled anthers as well as a subulate style. *Tyleria* is closely related to the three remaining American genera of the Luxemburgieae, all of which are herbaceous.

Hutchinson in his discussion of *Fleurydora* omits much of importance. In the first place he circumvents van Tieghem's tribe Godoyeae and shifts without explanation the type genus of the Godoyeae to the closely related tribe, Blastemantheae. In his description of the latter tribe he states simply that the fruit is a capsule. One of the striking characters of the genus *Blastemanthus,* a character which Hutchinson does not describe or discuss, and which in my opinion demands consideration, is the *reduction* in seed number to one or two per carpel; this condition is correlated with an infolding in the fruit of one or of both of the margins of each of the three carpels,

one of the paired margins being non-seminiferous (see figure 1, *h*); the seeds of *Blastemanthus* are exceptionally large and are nonalate (fig. 1, *j*). Thus in the character of its fruit *Blastemanthus* differs from *Godoya* and *Fleurydora*, as well as from the remaining American genera of the Luxemburgieae. In my opinion the internal structure of the fruit of *Blastemanthus* provides some evidence for upholding a distinct monogeneric tribe Blastemantheae. However I am retaining it in the tribe Luxemburgieae in light of the other characters discussed above.

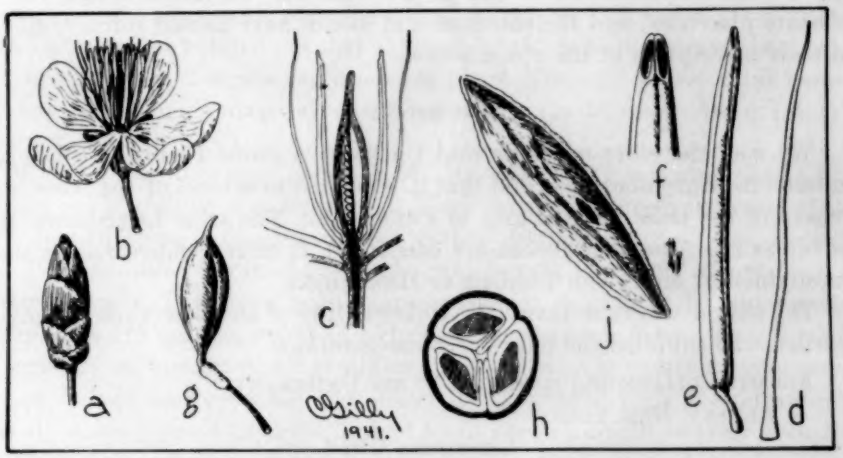

FIG. 1. *Blastemanthus grandiflorus* Spruce: a—bud (×1); b—flower (×1); c—longitudinal section through flower (×2); d—coronal segment (×4); e—stamen (×4); f—apical portion of anther, ventral view, showing dehiscence pores (×8). (a, drawn from *Spruce 2012;* b–f, drawn from *Ducke 297.*) *B. gemmiflorus* (Mart. and Zucc.) Planch.: g—capsule (×1); h—cross-section of mature capsule, showing placentation (×2); j—seed (×5). (g–j, drawn from *Spruce 3709.*)

To establish the relationship between *Fleurydora* and the genera of the Luxemburgieae is difficult. Several lines of evidence indicate that the New World genus *Poecilandra* is closely allied with Chevalier's genus; the leaf-blades are similar in shape, retuse at the apex, and have closely crowded secondary veins; the sepals are similarly disposed and comparable in texture, while the style is subulate, and the seeds are short-alate, although the wing in *Poecilandra* is about equal at each end of the oblong body of the seed. One important character, however, demonstrates that *Fleurydora* is related at least in part to the *Godoya, Rhytidanthera, Krukoviella, Cespedezia,* and *Luxemburgia* complex: the pattern of the placentation. Many workers (including Chevalier in his work on *Fleurydora*) state that the placentation is axial and hence the ovary is 3–5-loculate depending upon the number of carpels characterizing the particular genus. My observations show that the genera listed above have intrusive parietal placentation and that the

ovary is *uniloculate*. Although material of *Fleurydora* is not available for dissection, I anticipate that Chevalier in his figure of the cross-section of the ovary (see his figure 1, no. 9) has erred on the matter of placentation, as many authors have done in describing and figuring the ovaries of the genera of the above complex. I have found that the adjacent margins of the carpels pass into the locule in a paired condition and as they approach the axial "line" bifurcate, with each margin curving; a cross-section shows 3–5 T-shaped parietal placentae with the minute imbricate ovules borne on the abaxial face of each end of the T. Undoubtedly the thick-walled ovary, crassate placentae, and the abundance of ovules have caused workers to err in their description of the placentation.

SUMMARY

We may therefore conclude that Chevalier's genus *Fleurydora* belongs to the tribe Luxemburgieae and that it is related to several of the American genera of the tribe, particularly to *Poecilandra*. The tribe Luxemburgieae, as far as the American genera are concerned, is more comprehensive than maintained by either van Tieghem or Hutchinson.

The author wishes to thank Mr. Charles Gilly of the New York Botanical Garden who supplied the figure of *Blastemanthus*.

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ANOTHER NEW NAME IN VACCINIUM

W. H. CAMP

For a number of years it was customary to refer to the North American lowbush material of *Vaccinium* subgenus *Cyanococcus* having shining green leaves with sharply serrate margins and blue fruit as *Vaccinium pensylvanicum*. Later, it was pointed out that *V. pensylvanicum* Miller (Gard. Dict. ed. 8. 1768) referred to a non-vacciniaceous plant. The next oldest valid name for any part of this material was *Vaccinium angustifolium* Aiton (Hort. Kew. ed. 1. **2**: 11. 1789).

More recently Longley (Science **66**: 566–568. 1927) reported that *Vaccinium angustifolium* was tetraploid. Work now in progress indicates that "*V. angustifolium*" consists of two rather distinct entities, one diploid (n = 12), the other tetraploid (n = 24), which seem incapable of producing fertile hybrids. Therefore, such plants as might appear to be connecting intergrades are not the result of hybridization between these two followed by segregation, but the result of differential responses to environmental conditions. Where they grow together under the same conditions, the tetraploid is easily distinguished from the diploid by its greater height, coarser branching habit, larger flowers and leaves (the leaves are usually a deeper green), and much larger fruit. These differences seem to be the standard result of the advent of polyploidy in *Vaccinium*.

All of the available evidence points to the fact that the nomenclatural type of *V. angustifolium* Ait. belongs to the diploid population. It is therefore thought that some name should be found which might be applied to the tetraploid population. In searching through the literature, we find that Lamarck has given us an excellent description of this coarser plant, outlining in considerable detail the characters such as height of plant, size of leaf, flower, and fruit, which we now know serve to distinguish the tetraploid from the diploid, even noting that the plant came from Pennsylvania, where the tetraploid is relatively abundant.[1] Unfortunately, Lamarck applied the name *V. pensilvanicum* to his plant. In supplying a name for this tetraploid population, the following has been chosen:

[1] It is quite likely that the material sent to the Jardin du Roi—and from which Lamarck drew his description—was selected for size of berry, a natural thing to do. Several years ago I examined a plot containing more than a hundred of the late F. V. Coville's selections of "*V. angustifolium.*" These selections were made primarily on the basis of the size of berry. So far, each of these examined has proved to be tetraploid; and it was from this group of plants that the material studied by Longley was obtained.

Vaccinium lamarckii, Camp, nom. nov. *Vaccinium pensilvanicum* Lam. Encyc. **1**: 74. 1783. Not *Vaccinium pensylvanicum* Miller, Gard. Dict. ed. 8. 1768.

There is, of course, the problem of status. On the basis of the general morphological affinities, it might seem advisable to treat *V. lamarckii* as a genetic subspecies of *V. angustifolium;* but to do so might be laying the way open for a future cumbersome nomenclatural situation. For example: being tetraploid, the relatively lowbush *V. lamarckii* hybridizes freely with the highbush *V. corymbosum* in certain areas; in fact, as will be pointed out in later papers, it is the source of certain of the notable variant forms of *V. corymbosum.* On the other hand, genetically, it is completely disjunct from the diploid *V. angustifolium.* Actually, the apparent intergrades between *V. angustifolium* and *V. lamarckii,* the result of plants of both growing under unusual environmental conditions, are no greater in number and no more troublesome of identification than the "lamarckioid" segregates of *V. lamarckii* × *V. corymbosum;* yet we would not think of combining these latter two entities under the same binomial. It is therefore thought best to treat *V. angustifolium* and *V. lamarckii* as separate species, at least in the preliminary stages of our investigation. It has the further advantage, for the present, of clarifying the nomenclatural and phyletic situation in a group which contains differentiated and genetically disjunct pairs of diploids and derived tetraploids, such as: *V. caesariense* and *V. australe; V. atrococcum* and *V. arkansanum; V. pallidum* and *V. simulatum; V. tenellum* and *V. virgatum; V. torreyanum* ("*vacillans*") and *V. tallapusae;* as well as *V. angustifolium* and *V. lamarckii.*

THE NEW YORK BOTANICAL GARDEN
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INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Papers that relate exclusively to bacteriology, forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

The Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of three cents for each card. **The different subjects as classified below may now be ordered separately** (but no orders will be taken for less than one year's issue in any classification). Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

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